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THE UNIVERSITY OF ALBERTA

BEHAVIOURAL CHARACTERISTICS RELEVANT TO HANDLING AND DOMESTICATION OF UNGULATES

by

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A THESIS

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ABSTRACT

A multidisciplinary, primarily ethological study was conducted to investigate the behavioural responses of some domestic and non-domestic ungulates to handling and to captivity. Generally, the hypothesis being tested was that few if any species-specific differences in behaviour patterns and responses exist as significant deterrants to the domestication or husbandry of wild ungulates.

Paleo-ecological analysis and survey of archaeological literature revealed that several modern-day wild species had in fact been husbanded by early man (e.g. red deer, gazelle, moose). With the adoption of agricultural subsistence patterns, these species may have been ecologically, though it appears not behaviourally, unsuited to further domestication.

Ecological, social and physical traits of 138 ungulate species were analyzed statistically to determine to what extent animal trait variation had historically influenced probability of being selected for husbandry. It was found that classical domestic species generally weighed over 50 kg., were non-selective feeders in open-country and montane habitats, and were socially advanced, non-territorial, typically occuring in groups of 15-100 animals.

Experimental work with captive bison, yak and Hereford cattle revealed few major differences in adaptability to captivity and handling. Bison differed from Herefords in (1) specificity of habituation to familiar handlers, (2) greater importance of routine in handling, (3) higher level of alertness, and in (4) having stronger peer group bonds than cattle. Data obtained from other domestic and non-domestic ungulates supported these conclusions.

The final section of the study consisted of an ethologically oriented analysis of a large-scale bison vaccination program in Wood Buffalo National Park. Three problem areas were identified. (1) Crowding resulted in goring by adult males. (2) Confusion in the herd lead to cow-calf separation. (3) Capture myopathy was tentatively identified, with ambient temperature and speed of handling perhaps being the factors critical to the onset of capture myopathy.

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I found, somewhat to my amusement...that animals always behave in a manner showing the rightness of the philosophy entertained by the man who observes them.

-Bertrand Russel, My Philosophical Development

INTRODUCTION

The first ungulate domestication is generally credited with having taken place well over 10,000 years ago. In addition, it is most likely that other species had existed in some form of close relationship with man several millenia earlier. It is a curious fact, therefore, that little more than a dozen ungulates are today considered domestic species.

As interest grows concerning the potential productivity of native mixed-species grazing systems, it appears inevitable that new ungulates will be added to the ranks of those species husbanded by man. If these as yet non-domestic species are to be kept successfully, it is desirable that information be collected on the reactions of such ungulates to handling and management at whatever level of intensity that management is practiced.

This study was conducted in order to gain insight into some of the various problems posed by husbandry of wild ungulates. While being behavioural in focus, the scope of the study was broad, and the approach multidisciplinary. The work relied heavily on archaeology, economic anthropology and comparative psychology as well as ethology, wildlife biology and animal science.

Each section of the study is largely complete in itself, yet complements investigations carried out in other

sections. The first two chapters deal with the question of why so few species have apparently been husbanded by man. Chapter 1 I look at the issue from the point of view of human paleo-economics, while in chapter 2 I try to determine whether variation in ecological, social or physical animal characteristics significantly affect the proability of being selected for husbandry or of doing well in captivity.

The next two chapters deal with the behaviour of ungulates in captivity. Chapter 3 discusses ethological and psychological theory as it relates to the experiential and hereditary determinants of behavioural responses, the influence of domestication on behaviour, and the effects of handling and captivity on behaviour patterns in wild and domestic ungulates.

In chapter 4 are reported the results of a study carried out at the University of Alberta Experimental Farm. The experiments were designed to evaluate the responses of related domestic and non-domestic ungulates to handling and to identify other aspects of emotional make-up and inter-specific relationships pertinent to management.

The final chapter attempts to apply the concepts of ethology and comparative psychology to a large-scale bison handling operation in Wood Buffalo National Park.

CHAPTER ONE

EARLY MAN-ANIMAL RELATIONSHIPS

DEFINING DOMESTICATION

Webster's New World Dictionary defines domesticate as "to tame for man's use". Such a definition ,although close to most people's intuitive understanding of the term, oversimplifies the nature of the relationship. Taming is not a prerequisite. Range cattle, though considered domestic, are by no means always tame.

Several other criteria by which domestication should be measured, have been offered: that the relationship not constitute parasitism (Herre 1969); that the animals be kept under manageable conditions (Berry 1969); and that controlled breeding take place with the animals removed from their natural living area (Bobrowski 1977).

A definition can be useful in that it helps to conceptualize and to classify. In the case of early animal husbandry however, the use of the word domestication carries with it such inflexible connotations that many early forms of association between man and animals seem to have been ignored.

On the other hand, use of the expression 'animal husbandry' may permit a less confined outlook. It will be

seen that many instances of intensive man-animal relationships have existed which, although not entirely within traditional definitions of domestication, do embody aspects of husbandry and should be given greater consideration (Jarman 1972, 1976). For the purposes of this study, I will consider loose husbandry associations to be forms of domestication.

CONVENTIONAL EXPLANATIONS OF EARLY HUSBANDRY

The archaeological view of early animal domestication has traditionally held that a proper set of circumstances in the Middle East gave rise to the so called 'Neolithic Revolution' about ten to twelve thousand years ago (Table 1). The transition from collecting upland wild grasses to deliberate sowing and soil tillage led to a dramatic increase in food production, population, and in the sophistication of human culture - especially material (Reed 1960, Bokonyi 1976).

As technological changes took place, man was able to keep a large number of native ungulates in confinement. Gradually, due to isolation from wild populations and to the conscious or unconscious selection pressures of man, the newly domesticated animals began to diverge from the original population. Anatomical, physiological and behavioural differences eventually separated the two populations. Substantial time has been spent attempting to

TABLE 1. OLD WORLD DATING

APPROXIMATE DATE (years B.P.)	CULTURAL ERA (Middle East)	CULTURAL ERA (Northern Eurasia)	GEOLOGICAL ERA
3,500-2,500	Egypt	Bronze Age	Holocene
5,000-3,500	Bronze Age	Neolithic	(Recent)
12,000 - 5,000	Neolithic, Mesopotamia	Mesolithic	
	Mesolithic		
		Paleolithic	
35,000	Upper Paleolithic		
70,000	Middle Paleolithic	Paleolithic	Pleistocene
400,000			
	Lower Paleolithic		
1.75 million ±0.5 million			
			Pliocene

explain the relatively sudden change in the nature of man's contacts with local ungulate populations.

An "oasis theory" (Childe 1952) is based on the assumption that increasing aridity in parts of the Middle East at the end of the Pleistocene led to concentrations of men and animals in small pockets. In order to avoid extermination of the local ungulate species, a symbiotic

TABLE 2. SOME MODERN DOMESTIC MAMMALS: TRADITIONALLY ACCEPTED DATES OF FIRST DOMESTICATION

APPROXIMATE DATE (years B.P.)	SPECIES	AREA	SOURCE
3000	Reindeer	Siberia	Zeuner 1963
3500	Alpaca	Peru	Zeuner 1963
4500	Yak	Tibet	Leonard 1973
4800	Horse	Ukraine	Drower 1969
5000	Water Buffalo	Pakistan	Zeuner 1963
5000	Dromedary	Saudi Arabia	Leonard 1973
5000	Llama	Peru	Leonard 1973
9000	Pig	Turkey	Reed 1969
9000	Cattle	Eastern Europe	Higgs&Jarman 1969
9550	Goat	Iran	Bokonyi 1976
10400	Dog	Britain, Idaho	Higgs&Jarman 1969
10870	Sheep	Iraq	Bokonyi 1976

relationship developed between man and ungulate. Gradually, true domestication evolved.

Childe's postulation that man responded to the danger of over-hunting by changing his relationship with his prey does not seem very plausible (Reed 1960). We have only to look at recent extinctions to realize that society rarely

acts to protect its resources until it is too late.

Braidwood (1960) argues that at the threshold of the Neolithic, man had finally evolved to that cultural level at which animal husbandry could replace hunting as the primary method of animal resource exploitation. Man developed a better understanding of environmental relationships and hunting slowly was replaced by forms of animal husbandry as a more productive form of exploitation. The debatable premise seems to be that knowledge about the environment was poor among Paleolithic hunter-gatherers as compared to Neolithic farmers (Jarman 1976). However, it appears unlikely that the thousands of generations of hunters had not assembled and passed on information about the animals that were so important to their survival.

In trying to develop a more comprehensive approach, Reed (1960) integrated the concepts of cultural levels and environmental change and added the factor of appropriate animal behaviour. The proposition is that without a population of ungulates exhibiting the "trait of sociability", domestication might not have taken place as it did. Unfortunately the analysis goes no further.

Common to these ideas is the view that the Neolithic Middle East is the proper focal point of interest. Although the precise site of the first domestication is mostly a matter of where archaeological excavations have been most successful (Bokonyi 1976), there has been agreement that only in the area east of the Mediterranean and into Iran did

man's interaction with and knowledge of his environment reach that level of complexity and proficiency where the natural environment could be altered. The 'static-historical' model maintains that only in the milieu of the Middle Eastern Neolithic could the important transition to animal domestication have taken place. The argument has been that it is only there that the wild ancestors of present day domesticated ungulates (goats, sheep, pigs and cattle) occurred together (Reed 1969).

This world view leaves one with the impression that the domestication of animals was the brilliant invention of a 'cradle of civilization' from which cultural sophistication then radiated to other areas. It is a world view which likes its cultures and animals neatly categorized - hunters or farmers, wild or domestic.

Evidence is accumulating against this simplistic outlook. The Middle East, for example, can no longer be conceived of as the prime source of cultural innovation. Corrected radiocarbon dates show many elaborate European tombs and monuments to be older than the Pyramids and that a metal industry existed along the Danube, in central Europe, as early as 6000 B.P. (Renfrew 1976). This is earlier than the civilizations of Mesopotamia which date from circa 5000 B.P. (Renfrew 1977). The significance of this information is that we can no longer accept that innovations such as forms of metalwork or of animal husbandry arose only in certain cultural contexts. Instead it may be that they were part of

a much broader phenomenon of adaptation and experimentation.

NATURE OF THE ARCHAEOLOGICAL EVIDENCE

Most researchers argue that any speculation concerning pre-historic domestication of animals be should based on exacting analysis of the available archaeological data. Domestication, the argument goes, should not be assumed until proven. The evidence that archaeologists look for has traditionally consisted of:

1) The appearance of morphological changes in ungulate bone samples associated with human settlements (eg.smaller size, crowded or decreased teeth, hornlessness, changes in the fine structure of bones)

2) Faunal remains showing that a high ratio of immature animals were slaughtered

3) A high incidence of animal tracks or scats in the area of a human settlement

4) The appearance of tools associated with animal husbandry (Zeuner 1963, Drew, Perkins and Daly 1971, Bokonyi 1976)

Hypotheses based solely on the existence of a high ratio of immature animals are often criticized. Collier and White (1976), for example, point out that even natural predation is unlikely to leave a representative sample of each age-sex class. They conclude that a high ratio of immature animals is on its own, no evidence for

domestication, and that until more concrete evidence is supplied, the exploitation pattern should be considered to be that of hunting.

ALTERNATIVE INTERPRETATION

However, there are those who adopt a less rigid stand (Higgs and Jarman 1972, Wilkinson 1972a 1972b, Jarman 1976). They ask whether the factors which have come to be considered as critically important to the existence of animal husbandry are of more than local significance. As well, they propose that those Middle Eastern centres on which subsequent developments are thought to depend are part of a much more widespread occurence both in time and space.

Wilkinson, Higgs and Jarman offer an alternative hypothesis to the traditional 'static-historical model'. Wilkinson (1972a) maintains that the dichotomy between wild and domesticated animals and between hunters and pastoralists is an artificial one, especially when referring to populations five to fifty thousand years ago. Although it has some classificatory value, it more often works to disguise what is in fact a broad range of man-animal relationships. It is held (Higgs and Jarman 1972) that animal domestication did not emerge as a reslut of of post-glacial inventions designed to exert control over the environment. Rather their alternative hypothesis suggests that animal husbandry unfolded as a natural course of events

in which selectively advantageous changes were continuously being made by man in his relationship to the environment.

In other words the Higgs-Jarman-Wilkinson position is that animal husbandry did not arise during the last eight or nine millenia; but instead that its roots go back much further. The position I take here is that the process of domestication extended over several thousand years and that different parts of the ancient world had their own peculiarities that resulted in some form of animal husbandry.

Higgs and Jarman (1969) argue that when archaeological evidence demonstrates a major dependence on one or two species, then a very close man-animal relationship is as plausible as a hunter-gatherer exploitation pattern. This view rejects evidence of osteological change as being a crucial criterion of domestication. The argument of long standing has been that the altered selection pressures of man will quickly work to produce morphological changes in domestic animals (Berry 1969). But tradition not withstanding, many point out that in the prehistoric situation, complete reproductive isolation may have been not only difficult to achieve but perhaps undesirable as well (Jarman and Wilkinson 1972; Wilkinson 1972a). As a result, morphological change should not be expected. As was pointed out earlier, the Paleolithic may have seen a vast range of man-animal relationships. At the beginning of these associations, animals were more probably selected for

characteristics they possessed than for potential changes that might be made.

As well as looking further back in time than the Neolithic, it is also important to broaden the scope of inquiry to include species other than our present day livestock. Zeuner (1963) suggests that there was no benefit in domesticating additional species once a sufficient number had been brought under the control of man. But Zeuner may have very well been wrong in assuming that conventional domestic animals were the first to be husbanded by man. Increasingly, the evidence points to red deer (Jarman 1972), fallow deer (Jarman 1976), gazelle (Legge 1972), and musk oxen (Wilkinson 1972) as having had relationships with man very similar to that of sheep in some early Middle East sites (Table 3).

Perhaps what is needed is not so much an ever more critical analysis of osteological remains but instead a greater understanding of and feeling for the ecological relationships and pressures of man during the Pleistocene. In the future, animal husbandry may be viewed as a natural continuation of exploitation patterns based on intensive or specialized hunting. There will be no need to invoke the notion of unique inventions in the Middle East. Technological sophistication will lose its place as the *sine quo non* of animal domestication.

TABLE 3. EXPERIMENTAL DOMESTICATION AND POSSIBLE PRE-NEOLITHIC ANIMAL HUSBANDRY

APPROXIMATE DATE (years B.P.)	SPECIES	AREA	NATURE OF MAN-ANIMAL RELATIONSHIP	SOURCE
4500	Oryx Addax	Egypt	Fattened Ritual sacrifice	Smith 1969
5000	Onager	Mesopotamia	Draft purposes before horses came	Bokonyi 1976
2100-1600	Gazelle	Rome	Fattened	Zeuner 1963
4500	Gazelle	Egypt	Fattened	Smith 1969
10000-8000	Gazelle	Palestine	Nomadic herding	
2200	Moose	Ukraine	Draft, riding	Zeuner 1963
> 15000	Moose	Northern Eurasia	Controlled hunt, loose herding	
> 15000	Reindeer	Northern Eurasia	Nomadic herding	Sturdy 1972
12000-5000	Fallow Deer	Middle East	Loose to close herding	Jarman 1976
30000-6000	Red Deer	Europe	Controlled hunt to close herding	Jarman 1976

PREHISTORIC HUSBANDRY OF NON-TRADITIONAL UNGULATE SPECIES

The notion than man tried but was not successful in domesticating other species (Sims and Johnson 1972) is not supported by the archaeological record. As was mentioned earlier, where the data point to dependence on one or two staple resources, a close man-animal relationship embodying elements of husbandry is not unlikely (Jarman 1976). Also,

the misconception that if a species is domesticated, it will remain so, seems to have clouded the thinking of some.

It is too often taken for granted that only those species familiar to twentieth century farmyards have been domesticated in the past. Where faunal remains of several species are found in large numbers in a human sttlement, today's wild species are usually considered to have been hunted, while bones of swine or sheep, for example, are said to be evidence of animal husbandry. Watson (1969), for example, in his discussion of domestic animals of the Chinese Neolithic, points out that the most common ungulates found at sites of early settlements were pigs and spotted deer (*Pseudaxis hortularum*). But while the pig is listed among the "domesticable species", the spotted deer and the almost equally numerous Chinese water deer (*Hydropotes inermis*) are grouped as hunted wild animals. Osteological analysis revealed that all fell within the range of present day wild forms.

The assumption of a Neolithic invention of animal husbandry has unfortunately led to Paleolithic sites being ignored. It has been felt (e.g. Reed 1968) that the study of Paleolithic hunters would add nothing to our understanding of early animal domestication. But it is now becoming more apparent that the disregard for Paleolithic data was unfortunate.

Red Deer (*Cervus elaphus*)

A great numerical preponderance, both geographically and chronologically, as well as a mortality rate showing many more males killed than females suggests that red deer may have been husbanded in some way in the pre-Neolithic.

Examination of 165 Mesolithic sites in Europe has revealed that red deer and pig together constitute the majority of the faunal assemblage. When ranked in order of number of occurences at these same sites, the five most prevalent species were (in order of importance): red deer, pig, cattle, roe deer, and moose (Jarman 1972). In much of Europe, red deer were intensively exploited for 5000 years, and in parts of southern Europe ties may have lasted in the order of 50,000 years.

As in many other ungulates, young males represent a surplus whose removal from the herd will not jeapordize the survival of the local population. It is the bones of such young males that dominate the red deer faunal remains. In addition, studies have shown that each human group was associated with a particular red deer herd throughout the year (Jarman 1976). A significant discovery is that ivy may have been collected as winter fodder (Simmons and Dimbleby 1974).

During a period of roughly one thousand years ending around 6500 B.P., animal husbandry systems based on modern domestic species had spread from south-eastern Europe to the North Sea, except for portions of Italy. From that time on, the red deer declined in importance. Only recently has

there been a renewed interest in the red deer as a domestic animal.

Gazelle (Gazella gazella , Gazella dorcas)

During prehistoric times gazelles were very common in the Middle East. They represent more than a third of the total meat consumed during much of the early Mesolithic and Neolithic in Palestine, until about 9000 B.P. So far, the evidence for husbandry of gazelle during this era is not substantial. However, rock drawings do show gazelle being herded into corrals (Harding in Mendelssohn 1974). Analysis of slaughter patterns, the evidence used to demonstrate much of the early domestication of sheep and goats, suggests that gazelle may have been exploited in a similar manner. In addition, many sites show that a very high frequency of immature animals were killed (Legge 1972). The logistics of providing the meat supply for early Neolithic settlements also implies that a dependence solely on hunting would have been unrealistic.

Later evidence, from the Old Kingdom of Egypt shows gazelle (as well as ibex, oryx and addax) being stabled and led about with collars. It is known the animals were kept for fattening and perhaps sacrificed in religious ceremonies (Zeuner 1963). In one Old Kingdom tomb a hieroglyphic message records that the occupant owned 3,988 cattle and 1,135 gazelle (Smith 1969). However, the husbandry of gazelle was abandoned both in early Neolithic Palestine and

in Egypt in favour of more ordinary stock such as sheep and goats.

Fallow deer (*Dama mesopotamica* , *Dama dama*)

In Palestine, during the late Paleolithic, the fallow deer was one of the major resources for more than 50,000 years. Unfortunately, little information is available concerning the nature of the exploitation patterns. However there is one intriguing piece of data. Evidence indicates that the fallow deer was introduced into areas outside its Pleistocene range (eg. Cyprus) early in the Holocene along with importation of sheep and goats (Jarman 1976). One conclusion may be that the association of fallow deer with man was similar to that of sheep and goats. Towards the end of the Neolithic in Cyprus, the fallow deer declined in importance and only modern domestic species remained.

Moose (*Alces latifrons* -extinct Pleistocene moose)
(*Alces alces* -extant species)

The moose is a resident of the northern forests, and there are as a result little data left to us of its relationship with man during the Paleolithic or Neolithic of northern Eurasia. The moose was an important economic species in Scandinavia, Ukraine, Germany, and Britain during much of pre-Neolithic times (Jarman 1972). However, the first tangible evidence is from a silver vessel dated at circa 2200 B.P. found north of the Black Sea. It depicts a

woman milking a cow moose with an antlered male standing nearby (Zeuner 1963). In more recent times, the moose was known to have been tamed for draft and riding purposes up until the end of the eighteenth century in parts of Scandinavia and Russia. The early Canadian explorer Samuel Hearne describes the moose as the easiest of the cervids to tame, and records that they were often kept by fur traders at what is now Churchill, Manitoba (Moodie and Kaye 1976).

Why did these associations not evolve into ones resembling the close bonds modern man has with domestic animals? As agriculture gained importance throughout Eurasia, why were the indigenous species abandoned in favour of present day domestic species? No clear answers have emerged. Answers may lie with either the animals themselves or with the people who ceased to depend on them. The study of paleo-economics offers one explanation.

HUMAN ECONOMICS AND THE BEGINNING OF ANIMAL HUSBANDRY

A traditional assumption of prehistorians has been that the domestication of plants and animals allowed an immediate increase in food supply, an improved nutritional level and a more stable annual diet in a largely sedentary society. These conditions, in turn, led to escalated population growth (Sussman 1972). There are at least two good reasons to question this theory. The evidence indicates that most hunter-gatherers were not living in miserable half-starved

conditions, but rather enjoyed relatively stable food sources with considerable leisure time to spend on other activities (Bender 1975). In addition it seems that southwest Asian populations began to expand with the initial exploitation of wild cereal grasses long before the change to sedentary habits (Sengel 1973).

It may be that an understanding of prehistoric human demographic patterns gives the greatest insight into changes in human paleoeconomics (Sussman 1972, Hassan 1973, Smith 1976). During the Paleolithic and early Neolithic the human population remained fairly stable, with an annual growth rate of between 0.0007% and 0.0015%. By late Neolithic times, however, the growth rate had jumped to 0.1% (Hassan 1973). From contemporary data it has been estimated that hunter-gatherer groups averaged 25 persons each while among agriculturalists the range was 150-300 individuals (Hassan 1973). Demography oriented prehistorians tend to concur that a change in birth control practices (mainly infanticide) was the major factor leading to increased population growth (Sussman 1972, Hassan 1973).

How do these data bear on the question of the shift in human economics towards animal husbandry? In keeping with the data presented earlier, it seems that although forms of animal husbandry most likely existed far back in the Pleistocene, it resulted in no appreciable population increase. Generally speaking, early forms of husbandry employing present-day wild species preceded cultivation and

many instances even collection of cereal grasses (Jarman 1972,Sherratt 1972). In the ungulate based economies, high levels of cropping can hinder the ability of the ungulate population to reproduce itself. The highest possible cropping level effectively restricted the size and density of each local human population. It seems then that although the subsistence base of hunters was muchmore substantial than was thought, it nevertheless was not favourable to the concentration of large human populations, with a few exceptions (Smith 1976). Speculation has it that the same holds for primitive, pre-agricultural herders.

With the beginning of wild cereal grass collection in south west Asia, a direct relationship between labour input and return was realized (Sherratt 1972). Birth control could now be relaxed and population allowed to increase. As true cereal cultivation emerged, even higher population densities could be tolerated.

Hassan (1973) writes that the basis of the relaxation in birth control was "...the change in the pattern of ecological and cultural adaptation involving a new extractive technology which allowed a high population density, large local group size and greater food productivity leading to higher maximum potential population size."

With the emergence of sedentary cereal based economies, it is likely that cattle, sheep and goats were better adapted ecologically than other Middle Eastern species

having had close association with man such as fallow deer and gazelle. In Europe, deer based economies lasted much longer than those east of the Mediterranean. 7500 years ago, most of Europe consisted of large deciduous forests, and economies based on pigs and deer. While populations were low and the land forested, that particular exploitation pattern was profitable. However, by 6500 B.P., the pigs, sheep, cattle, cereal grain economy had spread from the Balkans to the North Sea (Jarman 1972). One possible explanation for this shift in exploitative strategy is that a climatic shift 11,000 to 8,000 years ago allowed the extension of the range of wild cereals to higher elevations and latitudes (Sengel 1973), thereby setting off the same chain of events in Europe as in south-west Asia. Fire may also have been an important agent in clearing forests and one which would favour the production of hard-grained cereals (Lewis 1972).

As in the Middle East, a degree of economic innovation allowed a population increase. In turn, new population pressures necessitated further economic innovation. The important point is that as the human population increased, forest areas were cleared and that under these altered conditions, caprines and cattle provided greater productivity than red deer (Jarman 1972).

Human paleo-economy must be seen as a dynamic part of the ecological system. It changed as ecological pressures changed. Europe adopted the economic patterns of the Middle East only after a more productive pattern of exploitation

was necessary and possible. Pigs were retained probably due to their flexibile habitat preferences and omnivorous food habits. On the other hand, red deer and fallow deer did not suit the altered economic patterns. As a result, they quickly declined in importance.

The points I have tried to make in this chapter are (1) that ungulate species other than modern domestic ones were most likely husbanded by man in pre-Neolithic times, (2) that the shift to modern domestic species can be explained by reference to changes in the patterns of resource exploitation of pre-Neolithic human societies, and that therefore (3) it is not necessary to invoke the notion that 'wild' ungulates are inherently unsuitable to close man-animal associations.

CHAPTER TWO

ANIMAL TRAITS RELEVANT TO DOMESTICATION

INTRODUCTION

Evidence indicates that no more than three dozen ungulates have been husbanded, yet roughly 187 species are recognized today. In the preceding chapter, the success or failure of ungulate species as domestic animals was analyzed largely from the human economic point of view. Explanations dealing with the discrepancy in the early organizational advancement of man in various parts of the world account for much of the conservatism in animal domestication. However, it has also been maintained that some species possess physical, ecological or behavioural characteristics that 'preadapted' them tc the transition from a wild to domestic state (e.g. Hale 1962, Bubenik 1971). The logical follow-up is a zoologically oriented analysis of domestic and non-domestic ungulates.

A tabulation of behavioural traits (Table 4) which enhance or impair the tranistion to domestic status was given by Hale (1962).

TABLE 4. TRAITS FAVOURING DOMESTICATION (HALE 1962)

Group Structure:
Large hierarchically structured groups
Males associated with females at least seasonally

Sexual Behaviour:
Promiscuous mating behaviour
Sexual signalling based on movements and posture

Parent-Young Ineractions:
Precocial young establishing species bond by imprinting at a very early age

Responses to Man:
Short flight distance favours the approach, attachment and eventual keeping and rearing by man

Food and Habitat Requirements:
Omnivory and adaptability to a wide range of conditions

Most artiodactyl and perissodactyl species satisfy Hale's requirements. As a result, a more detailed multivariate analysis was conducted in order to discover whether historical trends in animal domestication reflected patterns of animal trait variation.

ANALYTICAL METHODS

The approach of the study was first to collate existing information on fundamental physical, ecological and behavioural traits of the world's large herbivores and then to determine which traits distinguished species which were conventionally domesticated from those which were not or had been husbanded only temporarily.

Selection and Expression of Traits

Of the roughly 187 species within the orders Perissodactyla, Artiodactyla and Proboscidea, sufficient information was obtained on 138. Fourteen characteristics were selected. Each it was felt, would influence either the probability of being selected for husbandry, or of adapting to captivity.

Physical traits thought to be relevant to the analysis were typical BODY WEIGHT and body CONFORMATION. Conformation was scored on the basis of a cephalization index (Geist 1966) which reflected the relative proportion of the fore and hind quarters. The lowest score was awarded to species whose forequarters were smaller than the hind. The highest score was awarded to species with social signalling concentrated in the area of the head and forequarters. Geist (1966) writes that species with considerable cephalization of display are as a rule socially more advanced.

Ecological traits included FEEDING STYLE and preferred HABITAT TYPE. Habitat use was described in terms of nine habitat types distinguished for the most part by tree cover and productivity of vegetation. Feeding styles were based on a classification by Hofman and Stewart (1972). Seven categories were identified, ranging from bulk grazers through intermediate grazers and browsers to highly selective browsers.

Remaining predictors related mainly to social organization, although other aspects of behaviour were incorporated. A number of attempts, none entirely satisfactory, have been made to classify ungulate social systems. It was hoped that those traits selected here would help identify important differences in the typical nature and size of wild populations and differences in the sorts of relationships within the groups. Main sources were: Estes 1974, Jarman 1974, Leuthold 1977 and Owen-Smith 1977.

TYPICAL GROUP SIZE: Included as a measure of ability to coexist in large numbers in a relatively small area.

MALE MATING SYSTEM: Seven categories were distinguished, consisting of (1) territorial males, (2) semi-territorial males, (3) territorial pairs, (4) territorial harems, (5) nonterritorial harems, (6) rank within a herd, and (7) hierarchies among roving males.

SOCIAL UNIT COMPOSITION: Five categories were recognized as indices of sociability, (1) single animals, (2) pairs,

(3) nursery bands with bachelor groups and single males, (4) large aggregations with seasonal segregation of males, and (5) aggregations with little seasonal segregation of males.

SPATIAL ARRANGEMENT: Species characterized by (1) all purpose territories, (2) mating territories, and (3) non exclusive use of space were differentiated.

STRENGTH OF FEMALE ALLIANCE: Considered an index of the cohesiveness of the nursery unit, alliance was graded from (1) (loose) to (3) (stable). Strength of the nursery unit bond is significant in that it may reflect how a species would do in the captive situation where sibling groups are separated and brought together at the whim of the herdsman.

MOTHER-YOUNG RELATIONSHIP: Three patterns of mother-young interaction were identified (Lent 1974)- (1) offspring hiding and remaining still while the mother feeds, (2) offspring following mother and remaining by her side, and (3) mother defending offspring against predators - may overlap with categories (1) and (2). It was thought that each of these typical responses might influence ease of adaptability to captivity.

ANTI-PREDATOR STRATEGY: Four typical response patterns were selected- (1) avoid detection, (2) flight after detection but before attack, (3) flight after attack, and (4) threaten or attack predator.

The dependent variable was domestic status. Three categories were recognized.

1. Wild- no historical evidence that the species ever was

	MALE MATING SYSTEM	SOCIAL UNIT	TYPICAL GROUP SIZE	BODY WEIGHT	CONFORMATION (Cephalization of display)	FEEDING STYLE	HABITAT TYPE
1.	Individual territorial males	Single	1-3	0-10 kg.	Negligible	Roughage grazers	Desert
2.	Territorial pair	Pair	1-5	11-30	Moderate	Fresh grass grazers	Grassland/ flood plain
3.	Territorial harem	Nursery bands, bachelor groups	1-50	31-50	Extreme	Dry region grazers	Savanna
4.	Nonterritorial harem	Large herds, males seasonally segregated	1-100	51-200		Tree and shrub browsers	Bush
5.	Dominance rank in herd	Large herds, little seasonal segregation	100+	201-500		Fruit and foliage selectors	Forest
6.	Roving males			501-10,000		Intermediate feeders preferring grasses	Montane
7.	Intermediate territorial forms					Intermediate feeders preferring browse	Alpine
8.							Swamp
9.							Tundra

TABLE 5. Categories of each of the predictors used in the analysis.

husbanded, and no current attempts being made.

2. Transient/current experimental- those species having been husbanded at some time in the past but abandoned in favour of today's domestic species. Also included are those species currently undergoing experimental domestication.

3. Classical domestic- includes species that have been husbanded closely for at least the last 2000 years.

In addition to predictor traits, two controlling variables were included. The first was FAUNAL REGION since in different geographical regions the cultural motivation to domesticate animals was expected to differ as would the spectrum of choices. In other words, the possibility of a species being domesticated might simply be related to the cultural level and demographic pressures of the local human population, as described in the previous chapter. The second controlling variable, TAXONOMIC GROUP, was included since it provided a composite of all physical, behavioural and ecological traits. It could therefore account for additional traits which were not captured in the above variables. A listing of, and complete key to the data deck is supplied in the Appendix.

Statistical Treatment

The statistical technique used was that of Multivariate Nominal Scale Analysis (MNA), included in the Osiris III package at the University of Alberta Computing Services Center (Andrews and Messenger 1973). In brief, MNA provides a multivariate analysis of nominally-scaled attribute data in the context of a linear additive model. The program performs no tests of significance (although this can be determined), but instead provides statistics describing strength of association. Several types of relationships were investigated.

Generalized bivariate relationships:

The generalized eta-squared statistic describes how well a predictor, considered alone, explains variation in domestic-wild status.

Multivariate relationships:

The generalized R-squared statistic is roughly interpretable as a generalized multiple regression coefficient. It expresses the percentage of total variation explained by any group of predictor variables.

Marginal predictive power evaluates the contribution of any single independent variable above and beyond the variation explained by all other predictors.

Category-specific relationships:

The category specific eta-squared statistic denotes which predictor is most useful in distinguishing any one category of the dependent variable from the other two.

Category specific R-squared indicates which category of the dependent variable was best predicted by the independent variables.

Variable-specific response profiles were constructed to illustrate how each category of the predictor variables was related to each category of the dependent variable.

RESULTS AND DISCUSSION

Relative importance of ecological, social and physical traits to animal domestication

Variables were screened initially. FEMALE ALLIANCE, SCENT MARKING, ANTIPREDATOR STRATEGY, and MOTHER-YOUNG RELATIONSHIP were dropped from further analysis on the basis of their low eta-square scores. The remaining predictors were grouped into ecological, physical and social traits. Following the generalized R-squared data represented in Figure 1, combined ecological traits are shown to be slightly superior in proportion of total variance explained. The category specific R-squared statistic (Table 6), indicates that ecological traits were most useful in distinguishing each of the three dependent variable

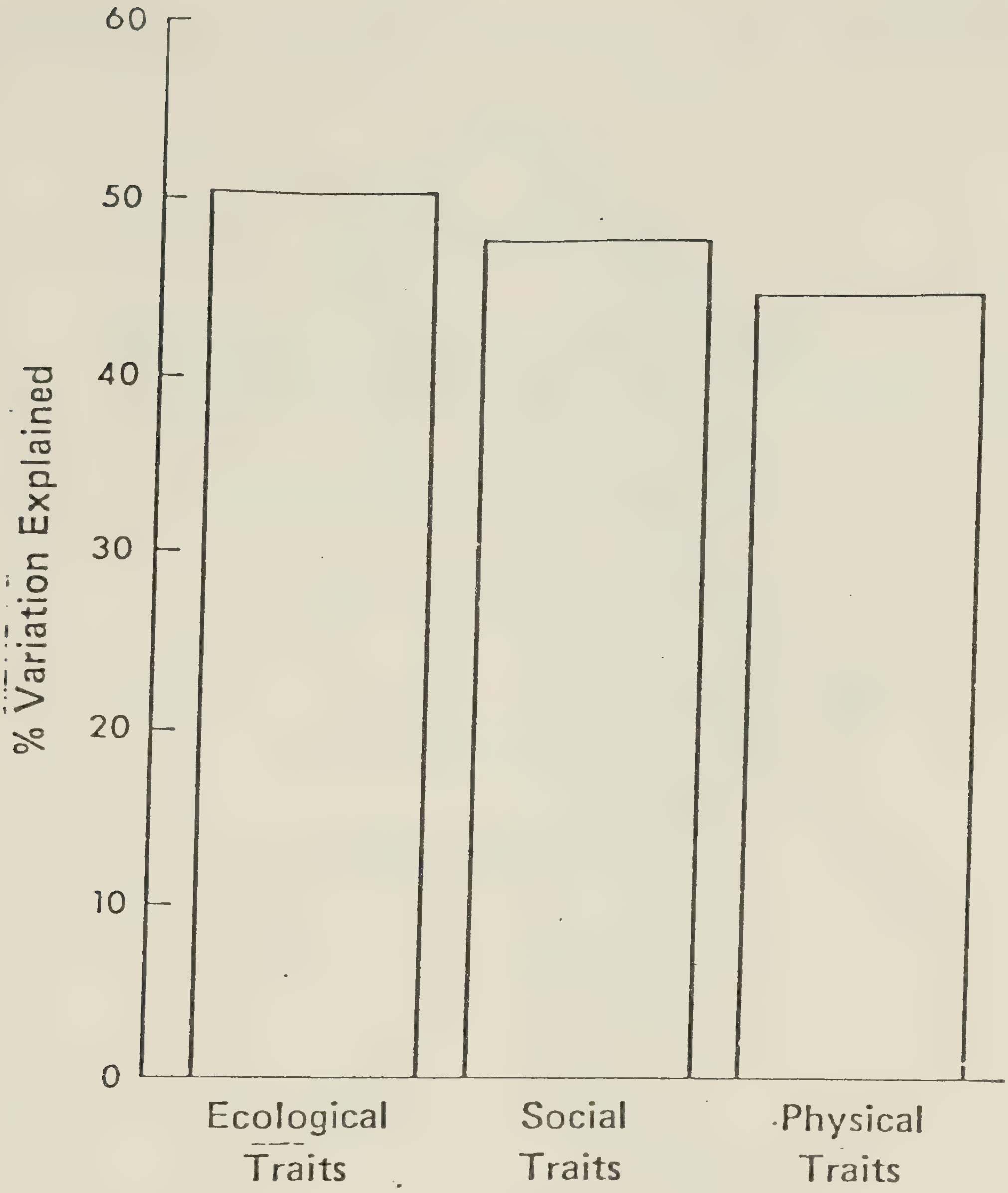


Figure 1. Represented here is the proportion of domestic-wild variation explained by Ecological traits (FEEDING STYLE, HABITAT TYPE), Social traits (MALE MATING SYSTEM, TYPICAL GROUP SIZE, SOCIAL UNIT), and Physical traits (BODY WEIGHT, BODY CONFORMATION).

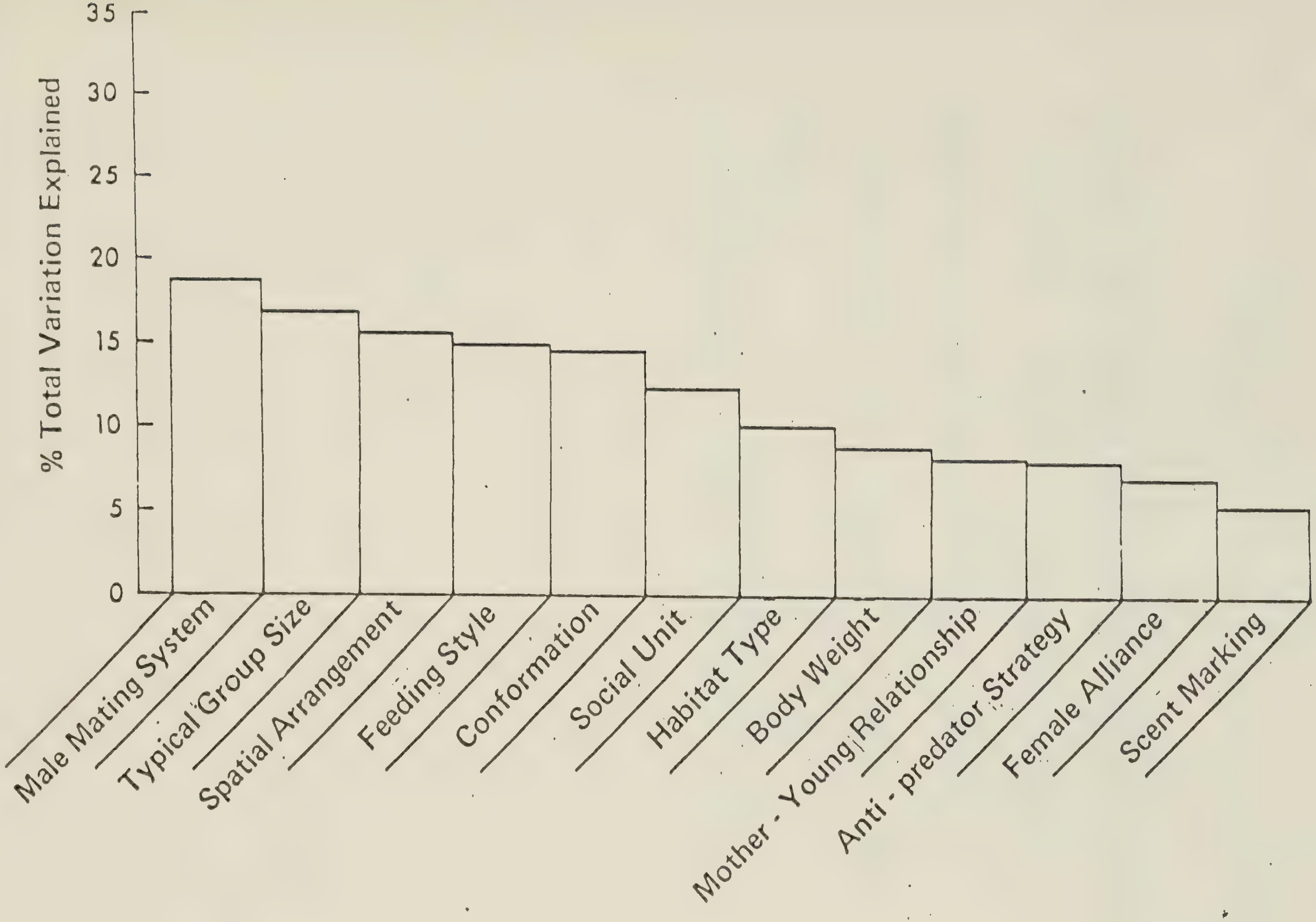


Figure 2. Ability of each single predictor trait, considered alone, to explain domestic-wild variation.

categories (wild, transient, domestic) from the other two.

TABLE 6. ABILITY OF GROUPED TRAITS TO DISTINGUISH EACH CATEGORY OF THE DEPENDENT VARIABLE FROM THE OTHER TWO.

	WILD	TRANSIENT	DOMESTIC
ECOLOGICAL TRAITS	39.54%	31.06%	39.61%
PHYSICAL	39.26	26.37	38.46 TRAITS
SOCIAL TRAITS	36.84	23.15	38.04

The superiority of combined ecological traits both in explaining total variance and in distinguishing each category coincides with the long held view that habitat and feeding preferences of modern domestic bovines and caprines 'preadapted' them for a symbiotic relationship with man as plant cultivation spread and forests were cleared. Browse oriented cervids were no longer favoured.

Explanatory value of single predictor traits

The apparent importance of individual traits depended upon the statistic being considered. Considering only the category-specific eta-squared statistic (Table 7), HABITAT TYPE appeared most important in separating domestic species from wild or transient species. In terms of explaining total domestic-wild variation (Figure 2) MALE MATING SYSTEM received the highest score. Yet the marginal predictive power (Figure 3), results in an entirely different rank configuration. Here, independent predictor variables are being evaluated on the basis of their contribution over and above the variation explained by the controlling variables TAXONOMIC GROUP and FAUNAL REGION. On this basis, FEEDING STYLE ranks as the most important predictor.

It is interesting that ability to distinguish domestic status is not closely related to ability to differentiate transient/experimental status. Table 7 indicates how well each catogory of the dependent variable was predicted by each of the independent variables. It is worthwhile noting

TABLE 7. CATEGORY SPECIFIC R-SQUARED. Indicates which category of Domestic Status was best predicted by independent variables.

	WILD	TRANSIENT	DOMESTIC
HABITAT TYPE	29.94%	16.04%	42.19%
SOCIAL UNIT	28.92	12.43	41.13
GROUP SIZE	36.15	20.21	39.69
CONFORMATION	41.13	29.06	39.56
BODY WEIGHT	31.30	11.56	39.03
MALE MAT. SYS.	30.19	9.35	38.52
FEEDING STYLE	41.18	26.37	37.68

that in each case, transient/experimental status was least well predicted. As such, it may be assumed that membership in the category is little dependent on definable or typical traits. The species in this category have been selected on quite diverse bases and it is reasonable that as a group, the member species have little in common. This ranking being entirely unrelated to that provided in Figure 2 can only be explained in that MALE MATING SYSTEM, for example, is closely correlated with both TAXONOMIC GROUP and FAUNAL REGION and therefore adds little explanatory power. On the

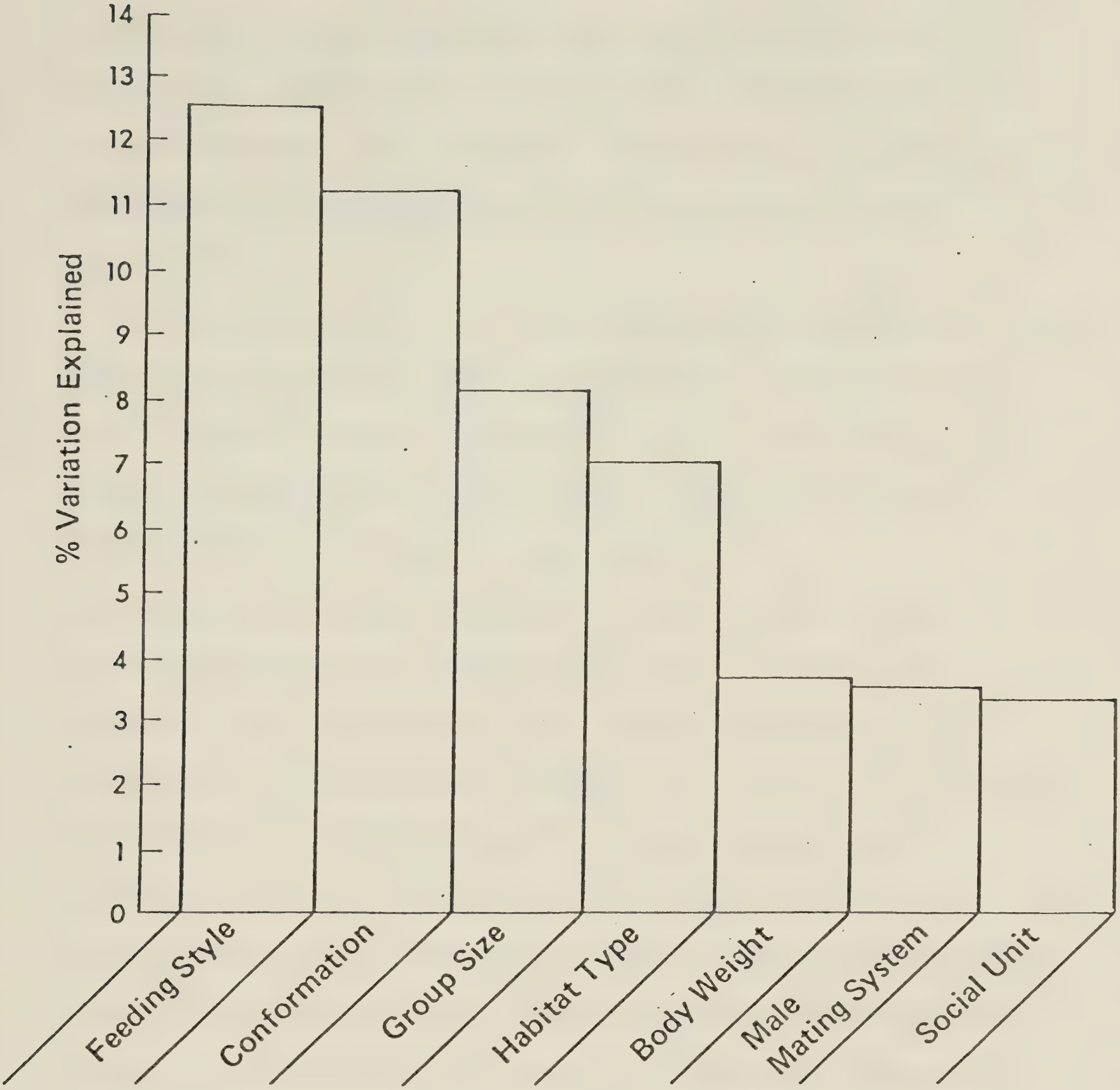


Figure 3. Marginal predictive power. Illustrates the percentage of domestic-wild variation explained over and above that accounted for by TAXONOMIC GROUP and FAUNAL REGION.

other hand, FEEDING STYLE and CONFORMATION must be considerably less closely related to either of the controlling variables. In other words, FEEDING STYLE may cut across taxonomic and geographic boundaries and provides an historically important index of likelihood of being husbanded.

The significance of CONFORMATION, a somewhat artificial classification, requires explanation. As was indicated, CONFORMATION is used here as an index of cephalization of display (Geist 1974). Of all the traits considered, CONFORMATION was the best predictor of transient/experimental status. Why was the extreme conformation type so common among transient domestic species? It was first of all thought possible that CONFORMATION might reflect muscle distribution in that less meat would be available from the hind quarter area. However, this is not the case. It appears (Berg and Butterfield 1976) that species such as moose, white-tailed deer and even bison, are relatively better developed in the muscles of the pelvis than cattle. From the standpoint of the modern beef breeder, these non-domestic species have a more desirable muscle distribution than cattle. So there is little reason to believe that species with high conformation scores were abandoned due to poor carcase yield.

A second explanation is offered. Low CONFORMATION scores indicate primitively social species, usually

occurring in small groups (Geist 1966). There seems little chance that these would be selected by man for husbandry. On the other hand, extreme CONFORMATION scores may imply that the animals are inconvenient or even dangerous to keep. Antlers, for example, reflect a strategy of high energy expenditure during a short rutting period. It is more than coincidence that male cervids kept in captivity most often have their antlers cut off. It may also be significant that wild sheep (also an extremely cephalized group) were quickly selected for reduced horn size after initial husbandry began.

Controlling variables

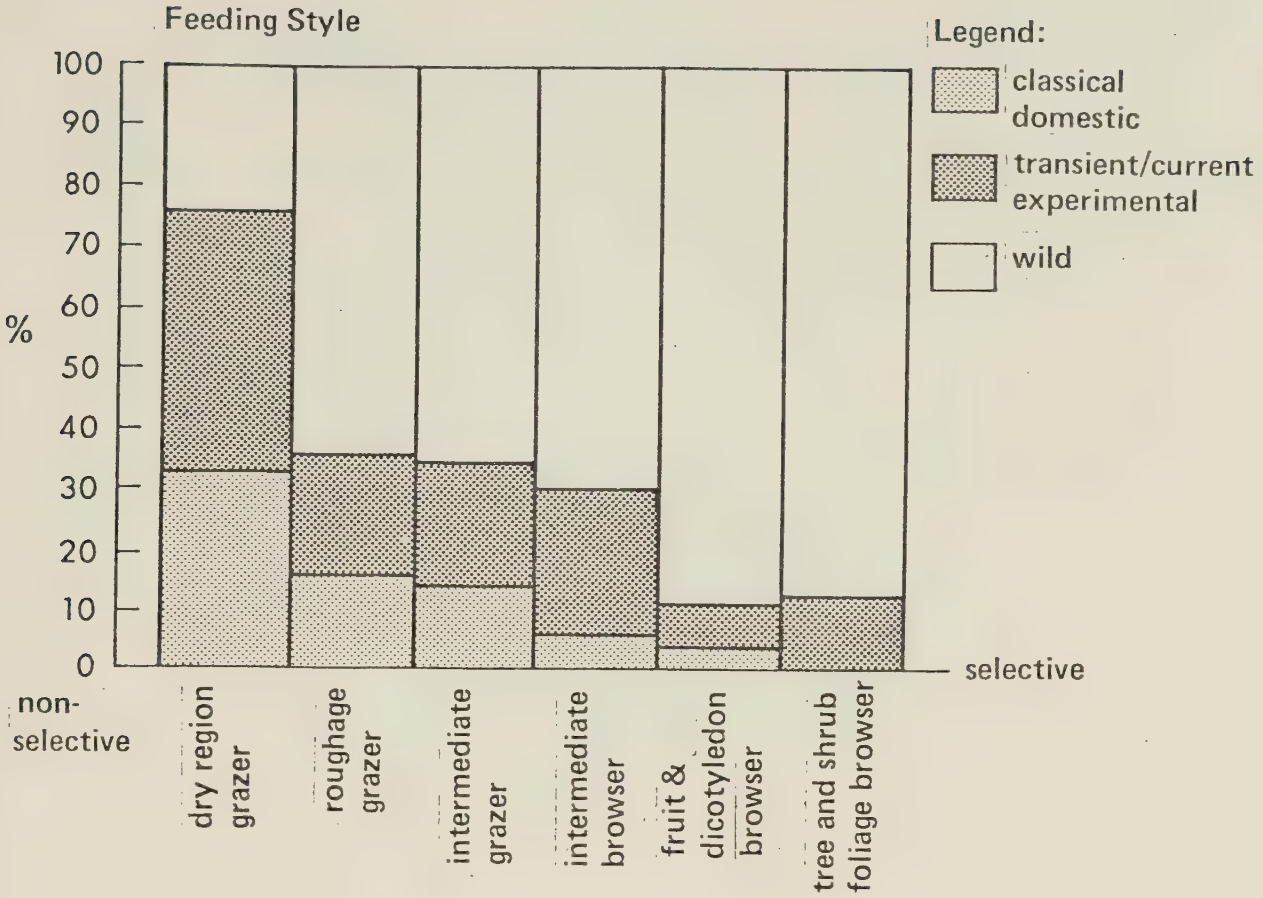
Not represented in Figure 3 is the fact that the controlling variables, TAXONOMIC GROUP and FAUNAL REGION when analyzed as predictors in the bivariate sense, both account for a higher percentage of the total variance than any other independent varables. FAUNAL REGION may best be considered a non-animal trait in that its high predictive value is associated with the coincidences of human geographic distribution and regional cultural development. That is not to say that patterns of faunal distribution are not related to ecological and social evolution. However, the phenomenon of domestication by man is so closely tied to human demographic and cultural evolution patterns that the significance of zoogeography lies in the geographic relationships of human and ungulate populations.

As for TAXONOMIC GROUP, close evolutionary ties are often manifested in the form of physical and ecological similarities, and by distribution within the same faunal region. As a result, successful domestication has in the past followed taxonomic lines. For example, members of the sub-families Bovinae and Caprinae and of the family Camellidae have been more frequently and intensively husbanded than any Cervid sub-families. In essence, taxonomic group is a composite of the twelve ecological, social and physical traits and that accounts for its high predictive value.

Variable specific response profiles

Variable specific response profiles for ecological, social and physical traits are presented in Fig. 4-6. As mentioned, the response profiles show how well each category of the seven predictor variables is related to each category of the dependent variables. The histograms in these figures are based on percentage distributions. Ecologically the trend has been for the non selective grazer to be favoured over the selective browser for husbandry and domestication. It should be apparent that the greater the omnivory and non-selectivity of a species, the greater the advantage to human populations. Again, this is reflected in the European Neolithic change from a deer-pigs forest economy to an agrarian one based on cattle and sheep.

Figure 4. The percentage distribution of each category of the dependent variable (domestic, transient, wild) with respect to the categories of the two ecological traits (FEEDING STYLE and HABITAT TYPE).


Feeding Style
Legend:
classical domestic
transient/current experimental
wild
%
100
90
80
70
60
50
40
30
20
10
0
non-selective
selective
dry region grazer
roughage grazer
intermediate grazer
intermediate browser
fruit & dicotyledon browser
tree and shrub foliage browser

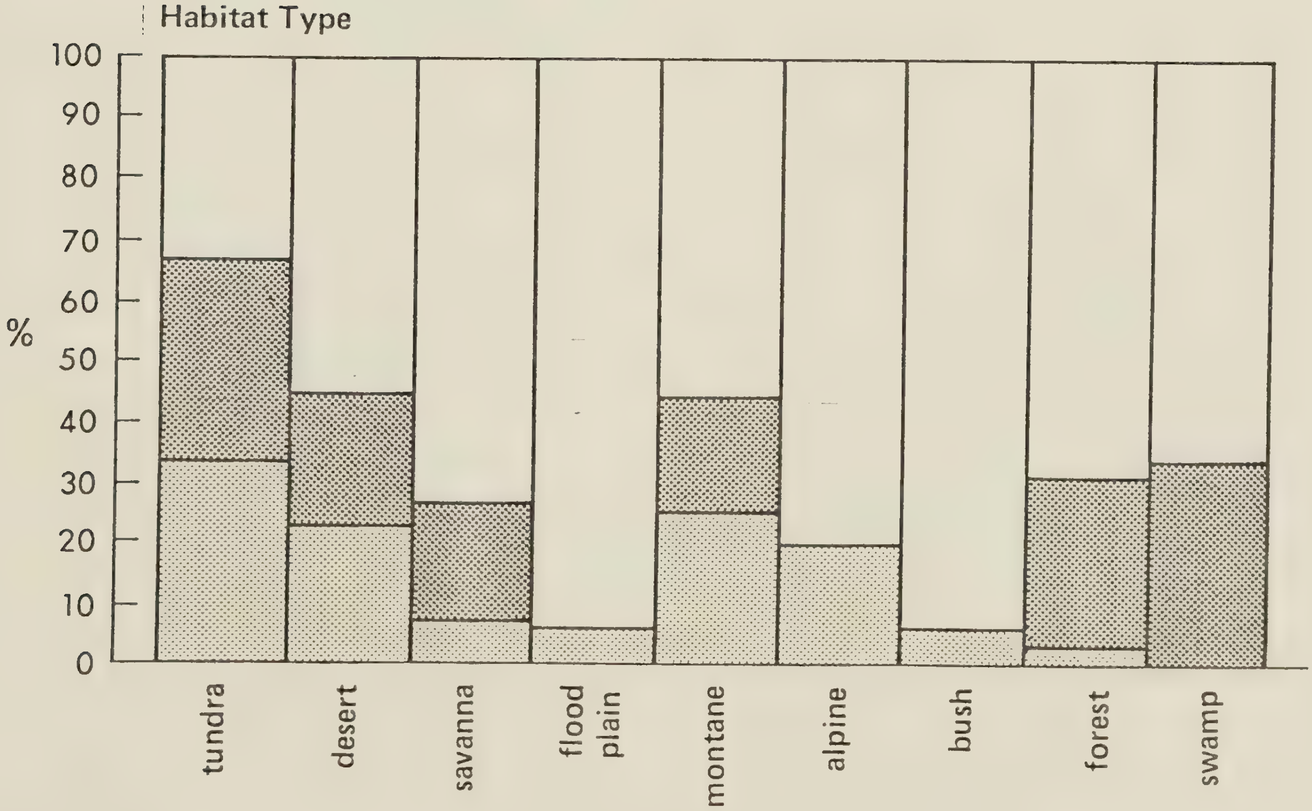
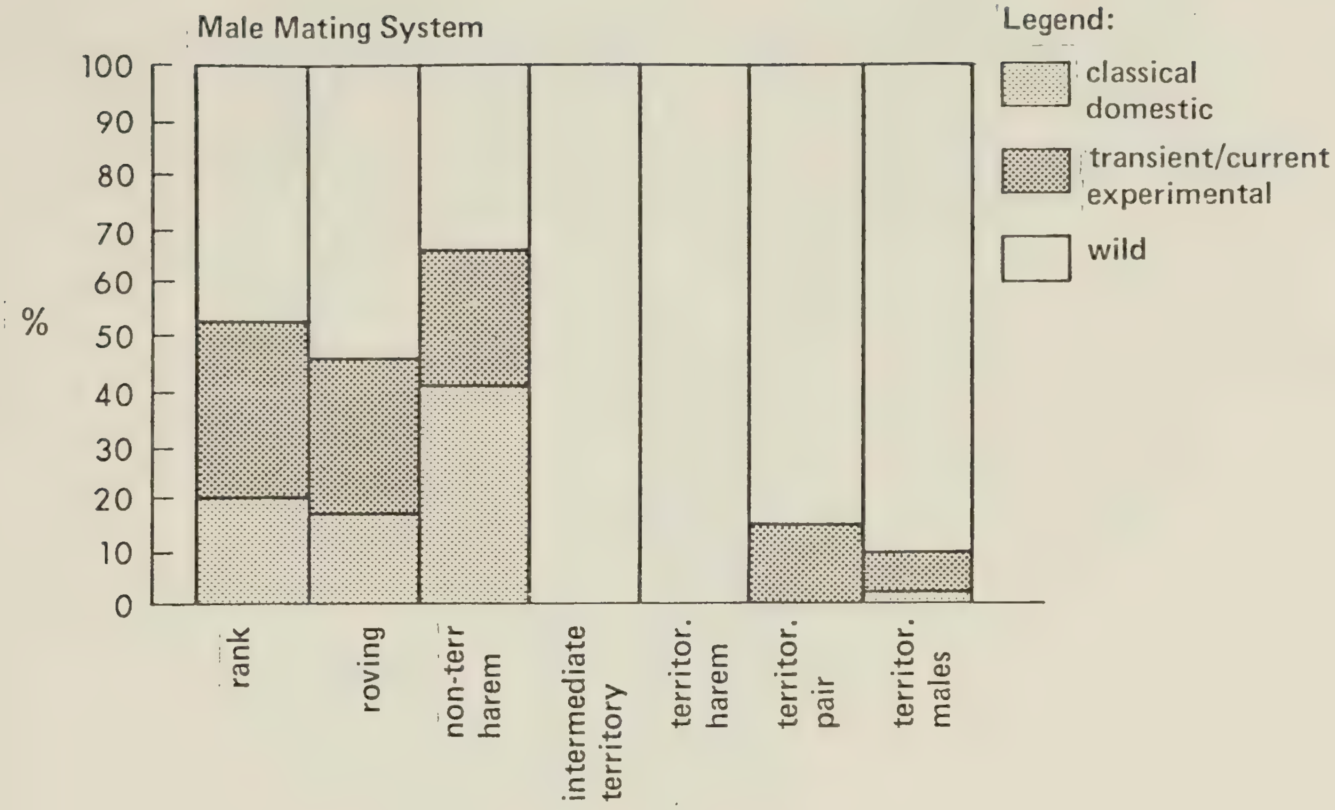

Habitat Type
%
100
90
80
70
60
50
40
30
20
10
0
tundra
desert
savanna
flood plain
montane
alpine
bush
forest
swamp

Figure 5. The percentage distribution of each category of the dependent variable (domestic, transient, wild) with respect to the categories of the three social traits (MALE MATING SYSTEM, SOCIAL UNIT and TYPICAL GROUP SIZE).


Male Mating System
Legend:
classical domestic
transient/current experimental
wild
%
100
90
80
70
60
50
40
30
20
10
0
rank
roving
non-terr harem
intermediate territory
territor. harem
territor. pair
territor. males

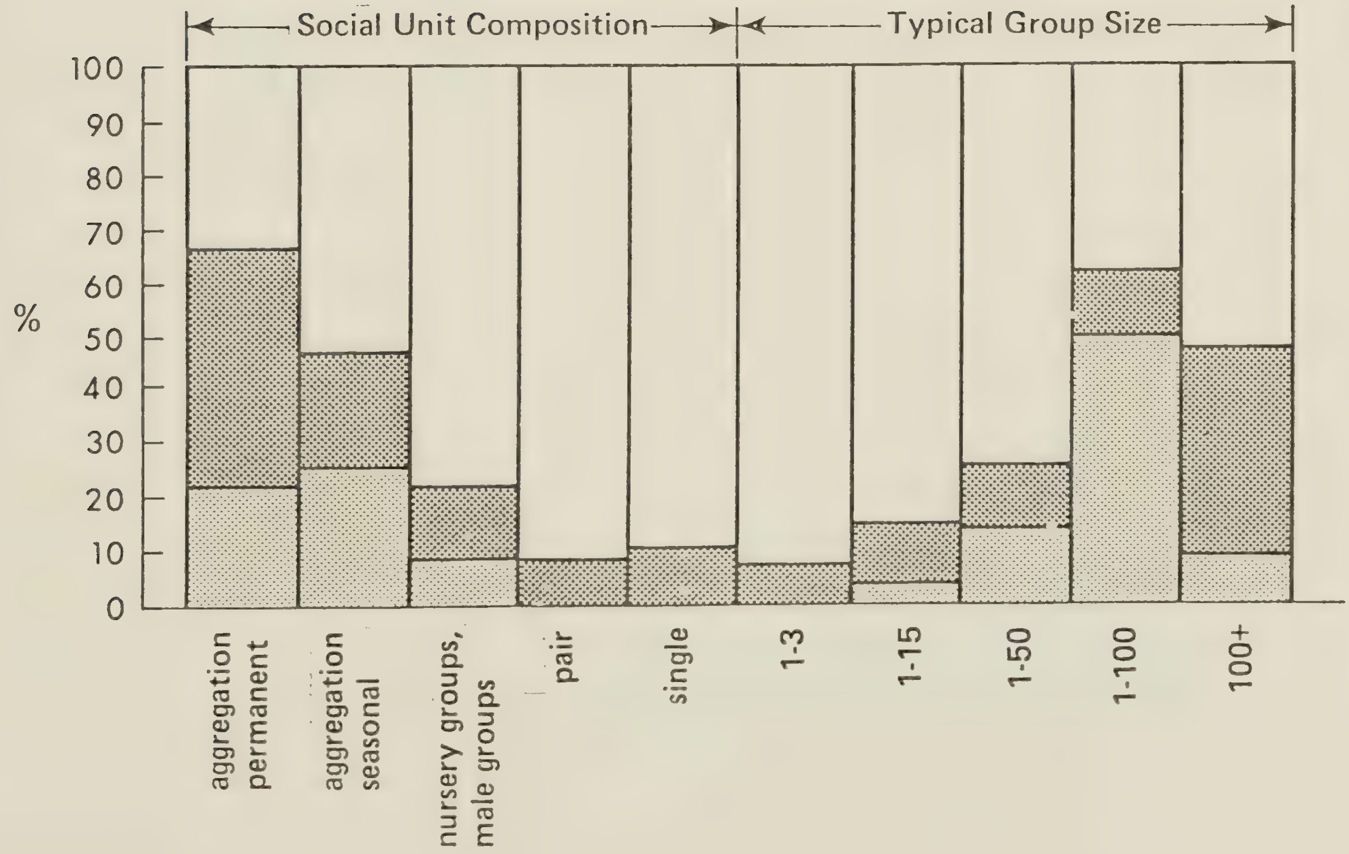
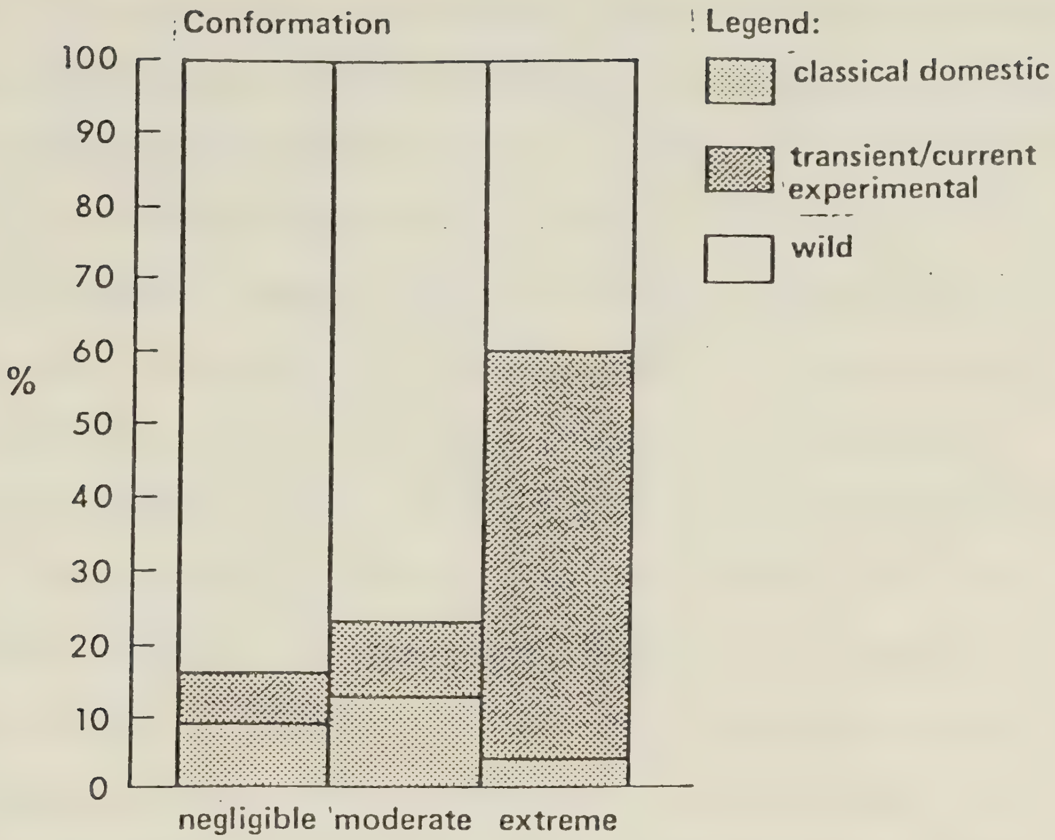
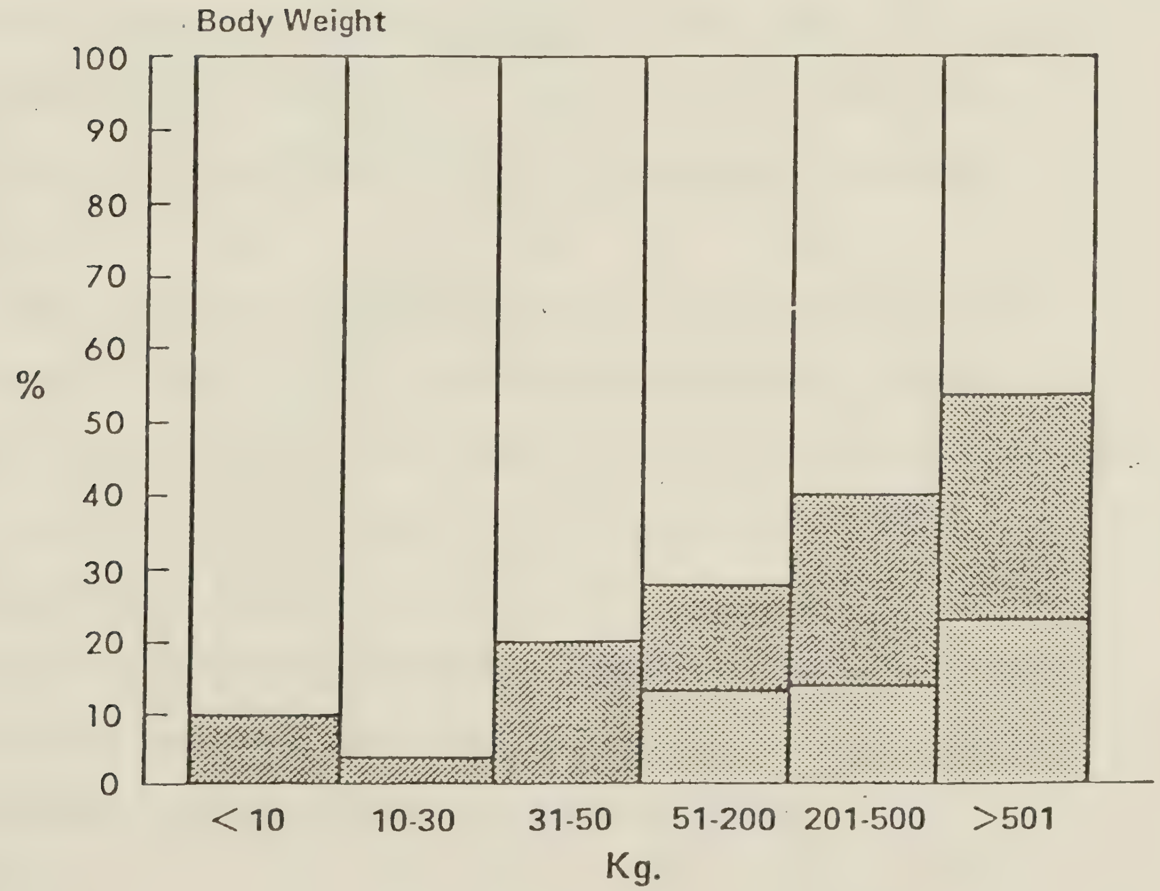

Social Unit Composition
Typical Group Size
%
100
90
80
70
60
50
40
30
20
10
0
aggregation permanent
aggregation seasonal
nursery groups, male groups
pair
single
1-3
1-15
1-50
1-100
100+

Figure 6. The percentage distribution of each category of the dependent variable (domestic, transient, wild) with respect to the categories of the two physical traits (BODY WEIGHT and CONFORMATION).


Conformation
Legend:
classical domestic
transient/current experimental
wild
%
100
90
80
70
60
50
40
30
20
10
0
negligible
moderate
extreme


Body Weight
%
100
90
80
70
60
50
40
30
20
10
0
< 10
10-30
31-50
51-200
201-500
>501
Kg.

HABITAT TYPE also reveals historically important trends. 'Closed' habitats such as forest, bush and swamp contribute a much smaller percentage of domestic animals than do most 'open' habitats. In neither of these ecological traits does the distribution of transient/experimental domestic species follow the same pattern. These transients appear significantly in closed as well as open-country habitats, and reflect the wide variety of situations in which husbandry has been initiated at one time or other.

It was assumed a priori that body weight would be an important criterion of domestic status. The results corroborated this assumption, and it is interesting to note that few ungulates species weighing on the average less than 50 kg. are represented among classical domestic animals.

Clearly, smaller ungulate species have been considered less potentially valuable. Again this pattern is not paralleled by the distribution of transient domestic species.

Quite obvious response profiles are evident with respect to social traits. MALE MATING SYSTEMS range from highly territorial to ones based on social rank hierarchies. Taken as a group, the three non-territorial systems make up a considerable majority of both the classical and transient/experimental domestic species. It may be that territorial species have difficulty adjusting to the confinement associated with modern husbandry.

TYPICAL GROUP SIZE and SOCIAL UNIT COMPOSITION both reflect levels of gregariousness. The tendency is for species normally associating in large groups to have been selected for husbandry. Solitary or otherwise primitive social species may be unable to maintain that level of social interaction necessitated by local crowding. On the other hand, it may simply be that solitary or only slightly gregarious species have been less likely to have been considered a profitable species in the early stages of animal husbandry. Initially, husbandry systems would have relied on natural population densities and food sources. Nevertheless, the evidently important dichotomies between territoriality and non-territoriality and between typically solitary and more gregarious species form the basis for the relatively high explanatory value of these traits.

Stability of behavioural components

Whenever reference is made to the possibility of behavioural obstacles to domestication, an important question emerges. Are species-specific behaviour patterns so stable that they will be retained in a largely unmodified form in captivity?

In the past, taxonomic classifications have been based on comparisons of behaviour patterns (eg. mating strategies or mother-young relationship). The assumption has been that these patterns have relatively high heritability. Analysis of feral populations supports this view. Rudge (1970) found

that the habit of hiding the newborn for two-three days, while the mother grazed, re-emerged among feral goats of New Zealand. Domestic goats do not display that pattern and domestic kids are considered to be "followers". However the "hider" strategy does exist in various forms among the more distantly related wild caprines. It has also been observed (Estes 1974, Leuthold 1977) that several species of antelope (e.g. kob, lechwe, topi,) can alter the nature of their territoriality in different environments.

Yet in spite of the return to supposedly ancestral pattern of organization by ungulates released from captivity, there is ample evidence of species-specific traits 'disappearing' or at least being modified after being brought into captivity.

Although consumatory acts (eg. eating, copulating) tend to remain fixed, the means by which that goal is reached may change in captivity (Thorpe 1956). The captive animal may learn new methods of finding food or a mate. Some species for instance, show conversion from pair-bond ordering to promiscuous mating (Kretchmer and Fox 1975). Furthermore, territorial behaviour tends to break down under domestication (Fox 1968). These alterations in normal social behaviour are often the result of husbandry methods relying on housing in small pens or otherwise crowded conditions. The difficulty lies in predicting just how behaviour will be modified under domestication. It is all the more disturbing when one realizes that whereas some changes are adaptive to

survival in captivity, others certainly are not. These issues will be dealt with in greater depth in the following chapter.

Interpretation

With any complex set of correlated traits, unambiguous rating is difficult. Sets of variables are more important than any one single predictor. Either HABITAT TYPE, MALE MATING SYSTEM, FEEDING STYLE, or TYPICAL GROUP SIZE could be considered the most important predictor depending on the statistics or group of statistics being used.

There are three distinct criteria which analysts use when evaluating the importance of any predictor (Darlington 1968, Andrews and Messenger 1974). The first is the simple, bivariate relationship. In this sense, MALE MATING SYSTEM provides the greatest degree of insight. The second criterion is concerned with marginal predictive power. In this case, how much of the variation in domestic status can a particular predictor explain over and above that explained by the controlling variables? According to this ranking, FEEDING STYLE is number one.

The last criterion asks how a predictor relates to domestic status if other variables, in this case the controlling variables, are held constant. This category-specific rating (beta-squared) identifies HABITAT TYPE as being most closely correlated with classical domestic status. However, it is not mathematical criteria that will

meaningfully explain the relationship between animal traits and animal domestication. In order to properly interpret the data it is important to understand the various historical contexts within which animal husbandry began.

CONCLUSION

The analysis performed here has centered on historically important characteristics. What has been determined is that certain animal traits have historically favoured successful domestication.

Physical traits: Large body weight (>50 kg.)
Ecological traits: Non-selective feeders
occupying open-country and montane habitats
Social traits: Socially advanced, non-territorial
species typically occuring in groups
of 15-100 animals

Yet data pertaining to transient or experimental domestic species does not follow this pattern. Perhaps the most significant observation is that no clear pattern emerged. Selective and non-selective feeding, open and closed habitat, territorial and non-territorial, gregarious and solitary, each is represented among animals having been husbanded at some time in the past. At this point it is interesting to re-examine Hale's (1962) criteria concerning the suitability of species for domestication. For ungulates,

it appears that his conclusions about group structure, food and habitat requirements, and sexual behaviour are in agreement with my own. Unlike Hale, I did not ,in this analysis, try to characterize response to man. It seems unrealistic to generalize concerning behaviour so profoundly influenced by experiential factors. On the whole, Hale's requirements still stand, but as I argued earlier, his categories are too broad to be of help in discriminating between ungulate species. Nevertheless, Hale does include the evidently most important past criteria, namely that species be socially advanced and ecologically flexible. As well, it cannot be overemphasized that patterns identified by this analysis have been of historical importance only. It would be a mistake to attempt future predictions based solely on historical trends.

It is becoming increasingly clear that today's popular domestic animals reflect in part the ecological biases of our agricultural system, its traditional and economically optimum management techniques. Through time, man's economic needs have changed, and as needs changed, so did the animals upon which he relied. The historical record points to a wide variety of species having been husbanded in some manner. The evidence seems to be that species were selected or abandoned on the basis of whether their food/habitat requirements provided an efficient mode of exploitation under the economic system that prevailed at any one time (Jarman 1972, Lewis 1972). It is important to understand that while

ungulates can be quite malleable in their habitat, social and other requirements, man is even more so. Extreme and necessary adaptations of groups such as the Saharan camel nomads (Gauthier-Pilters 1974) represents a form of man-animal relationship no more contrived or unnatural than that of the Western rancher and his cattle. In summary, success in domestication must depend on the suitability of the husbandry techniques being used.

CHAPTER THREE

UNGULATE BEHAVIOUR
-A THEORETICAL INTRODUCTION

INTRODUCTION

In the previous chapters, two arguments were made: (1) that many non-traditional species had been tamed or husbanded in some manner by early man, and (2) that few so-called species-specific characters, whether they be behavioural, ecological or physical, have prevented ungulates from having been successfully husbanded. Nevertheless, the conventional view is that 'wild' and 'domestic' animals are intrinsically different in their potential for habituation to man and in their ability to adapt to captivity.

The purpose of this chapter is to deal with such issues on a theoretical basis. Topics dealt with include effect of domestication on behaviour, the relative importance of hereditary and environmental influences, the importance of early experience to later behaviour, and problems posed by the captive environment.

THEORETICAL PREMISE

In theory, the basis of ethology should be the objective description of animal behaviour. Yet for an account to be more than simply anecdotal, it must be interpretive. In order for an interpretation to be meaningful, it must have its basis in some comprehensive theoretical framework. Behavioural measurements and descriptions, especially when taken outside the natural setting, are of little value unless interpretations have a theoretical basis.

Too often, data from the measurement or observation of behaviour are presented either in raw form or accompanied by superficial explanations and interpretations. This is true of 'statistically significant data' as well as of anecdotes. Denenberg and Banks (1969) illustrate the point by comparing the disciplines of physiology and ethology. In physiology, the significance of data is usually obvious, but the techniques are often very difficult to master. On the contrary, behavioural data are available to anyone. It is interpretation which requires expertise. As a result, presentation of my data is preceded by a discussion of behaviour theory as it applies to ungulate behaviour, its ontogeny and its modifications while influenced by the conditions of captivity.

Instinct and Learning

Schneirla (1972) defines instinctive behaviour as "...any species-typical patterns of response not clearly habitual or acquired through experience." Bees, for example, are able to perform highly complex programs entirely within the framework of instinctual control.

It is a common assumption that animals possess an innate nature modified at best only secondarily by the experiences of the individual. The fixed action patterns found in many invertebrates and vertebrate species illustrate this type of response to environmental releasers. These responses are inherited, and highly resistant to change. The role of learning is non-existant or at best minor.

However, the animal kingdom represents a continuum in the processes by which responses are made to environmental demands (Scott 1969, Brookshire 1976). At one end are those species displaying solely the rigid, stereotyped fixed action pattern. At the other end are the animals "...not guided by instinct, who must learn a whole series of complicated procedures from their parents, and who must be prepared to solve problems on their own." (Fichtelius and Sjolander 1973)

In vertebrates, the evolution of the brain (especially the cerebral cortex) has been associated with an increase in behavioural plasticity (Langer 1971, Fichtelius and Sjolander 1973, Welker 1976). Among those species

characterized by a long life span, wide geographic distribution, and a broad and complex ecological niche and life-history strategy, the likelihood of genetically unpredictable situations arising is high. This is the trend within several mammalian orders: rodents, ungulates, carnivores, primates, and cetaceans. The result is that simple genetically pre-programmed responses may be disastrously maladaptive (Marais 1939, Brookshire 1976). As Allyn (1974) states: "Exclusive genetic control of complex interactive systems is probabilistically more dangerous than that of simpler systems."

Throughout the intermediate phyletic levels are the various combinations of genetically coded and learned behaviours. With the evolution of learning the genetic coding of responses became very complex (McBride 1971). Genetically programmed reactions were no longer unalterable. Environmental feedback became an important factor. Responses were now retained only if reinforced positively. The ability to learn achieved high selective value. The position adopted here then, is that among the most advanced mammals (primates, cetaceans), the ability to learn is the basic genetic element.

However, I do not want to create the impression of a strict dichotomy between 'innate' and 'learned'. Among most mammals, certainly ungulates, any species-typical behaviour patterns are likely the result of environmental influences interacting with genetic-physiological processes at all

stages of ontogeny (Skinner 1966, Lehrman 1970).

Importance of Early Experience

A considerabe amount of published literature is available on the effects of early experience on later behaviour. Most work has been conducted in the laboratory with dogs, chickens, rats and mice. With few exceptions (eg. Donaldson et al. 1966) not much attention has been paid to ungulates. Research on laboratory rats has shown that early experience has an influence on: gregariousness (Ashida 1969), aggressive behaviour (King 1969), stereotyped behaviour (Fox 1965), open-field behaviour (Henderson 1967), and predatory behaviour (O'Boyle 1977). My concern is primarily with the effect of early experience on emotionality. Some research suggests that emotional reactivity is inversely proportional to the amount of stimulation during early development (Goldman 1969, Melzack 1969).

On the neuro-physiological level it is now accepted that the central nervous system changes functionally and morphologically during ontogeny. The change is such that the neurons become progressively less malleable (Horn, Rose and Bateson 1973) . The nervous system can also be altered by environmental influences during development. "The early effects apparently set or 'tune' the developing neuro-endocrine system...so that in later life, the threshold and duration of emotional and stress reactions...are altered."

(Fox 1970) This may be the pathway by which handling stress early in life seems to affect adult behaviour.

The implications are well known. Young animals are generally more malleable than adults. It is therefore during this early influential stage that every individual must first of all become socialized to his own species and later learn to cope with the demands and stresses imposed by his own environment. This has important and obvious ramifications for animal husbandry.

The imprinting process first recognized in birds, is now accepted as taking place in ungulates as well (Collias 1956, Smith 1965, Hess 1973, Gilbert 1974). Ungulates are among the most precocial of mammals (Lent 1974), and the critical period for making species attachments seems to be somewhere within the first twenty-four hours after birth. The exact number of hours varies considerably from species to species, but it is generally true that there are periods in an ungulate's very early post-natal development when it is very easy to change the animals to which a newborn becomes socialized, and later periods when this is more difficult or impossible.

Influence of Domestication on Animal Behaviour

"Selection by behaviour led to the hereditary reorganization of behaviour, with the result that previously wild animals became domesticated and some of them...even

friendly to man." (Belyaev 1969)

Referring to moose, Knorre (1974) writes that behaviour of animals "...raised under domestic conditions reflects entirely the training and regimen under which they are used to being kept."

The many and varied effects of domestication on behaviour have long been recognized (Hale 1962, Fox 1968, Kretchmer and Fox 1975). But it must be remembered that the behaviour one observes in livestock differs from that of non-domestic counterparts not only due to genetic changes brought about by artificial selection, but also because the animals may have been reared in captivity or otherwise subjected to influences quite different from those of the natural environment. The crucial question here concerns the extent to which artificial selection has indeed produced ungulates whose behaviour differs from that of related wild species. What are the effects of a prolonged selection for adaptability and docility?

Contemporary theories suggest that genetic alterations may be limited in their influence on mammal behaviour to (1) neoteny through a retention of neuron plasticity to a later age and (2) changes in nervous system thresholds such that responses are only elicited at higher stimulus levels (Murphree and Dykman 1965, Horn, Rose and Bateson 1973, Brookshire 1976, Welker 1976). The possibility of genetic

coding in advanced mammals for more specific behavioural responses remains a hotly debated issue.

Darwin (1859) originally conceived of domestication as a rapid form of evolution. As species became more and more dependent on man and less able to survive in the wild, both morphological and behavioural changes took place. Selection for adaptability and docility may have had the most pronounced effect on behaviour. Selection for adaptability favours neotenic individuals (Kretchmer and Fox 1975). Neoteny, since it results in the malleability of youth being retained later in life, would naturally be an advantage in captivity, both for the animal and the herdsman.

Artificial selection also stresses docility. Tameness may be largely a product of early experience, yet genotype does play a role. It may, however, be more likely that artificial selection modifies behaviour by changing neural thresholds (Hale 1962) than by selecting in effect for new gene combinations that specifically code for certain patterns of behaviour. In other words, the stimulus threshold needed to elicit a response has become greater in domestic than in wild ungulates.

A second class of behavioural changes due to domestication is the result of adaptations animals must make to the conditions of captivity. As mentioned in the preceding chapter, territorial behaviour can break down under domestication and captivity. In addition, it has

been suggested (Eibl-Eibesfeldt 1970) that domestication leads to overall simplified behaviour patterns.

The Captive Environment

Behavioural problems encountered with traditional domestic stock such as abnormal sexual behaviour, increased aggression and neurotic behaviour can be highly accentuated in non-domestic species brought in from the wild for purposes of research, exhibition, or meat production.

Three characteristcs of the captive environment stand out as a source of behavioural problems. These are crowding, handling by man, and a frequent poverty of environmental stimuli, also referred to as ethostasis (Fraser 1974). It is widely accepted that psychological stress can be brought on by an environment providing too low a level of stimuli as well as one forcing too high a level (Fox 1968, Fraser 1974, Fraser, Ritchie and Fraser 1975). Conventional wisdom holds that to each of these circumstances, domestic farm animals are better adapted than non-domestic ungulates.

Concept of stress

The term 'stress' has long been accepted (Fraser, Ritchie and Fraser 1975) as a convenient label to describe the results of interaction between an individual and various physical and social forces ('stressors') acting on that

individual. Traditionally, the view seems to have been that stressors should be avoided - the fewer the better. Such may not be the case. Fraser et al. (1975) argue that stress cannot even be considered a single phencmenon, but rather a dissimilar assortment of processes.

Selye (1956) found that a wide variety of physical stressors resulted in certain physiological responses collectively referred to as the General Adaptation Syndrome. When the connection between neuro-hormonal responses and the General Adaptation Syndrome had been made, behaviour researchers began using the stress concept in their analyses. The term has often been used quite loosely to account for any physiological or behavioural abnormality that cannot otherwise be explained. Behaviourally the term has remained confusing and ill-defined to the point where some workers (eg. Kiley-Worthington 1977) insist that use of the expression is of little value in understanding animal-environment interaction. Nevertheless, the expression does pervade the literature, and does provide some intuitive insight. Therefore, it will continue to be used here.

Recognizing that no single phenomenon exists, Fraser et al. (1975) tentatively define an animal as being in a state of stress if it becomes necessary for its physiology or behaviour to be altered beyond normal limits in order to cope with aspects of its management or environment. Such a definition, although still ambiguous, encompasses the stress due to both monotonous, stimulus-deficient environments and

situations characterized by crowding and frequent handling. Each will be described briefly.

Handling

Very few generalizations can be made about the reactions of ungulates to handling. So much depends on the tractability and degree of training of the animals. Practically speaking, most herdsmen probably learn what does or does not work in connection with handling their animals. However, the correct handling of animals has always been somewhat of an art, and much of the philosophy behind applied animal ethology has been that through ethological principles, the basis of the art may be spread to others.

Little data are available to document the effect of animal manipulation related stresses on physiology or behaviour. Yet some examples such as the well-known shipping-fever complex exist. Reproduction may be another area where management stresses have a pronounced influence (eg. Moberg 1976, Kiley-Worthington 1977).

Attempts to outline optimum animal handling or management techniques (eg. Squires 1975, Zeeb 1976) have usually emphasized understanding species-typical behaviour patterns. From there it was argued that systems should be designed so as to allow normal development and functioning of those patterns.

More specific examples of the results of poor

stockmanship, such as nervousness and poor milking performance by dairy cattle, injury to beef cattle during handling, or incorrect training of horses so as to render them unridable, show that losses in time and money can be prevented by a proper understanding of behaviour (Grandin 1974a,b, Kiley-Worthington 1977).

When dealing with animals that have been socialized to man and trained from an early age, handling poses few problems. However the presupposition made here is that animals must frequently be moved against their will. In this circumstance, handling can pose a considerable psychological and physiological stress.

Mixed species groups

Forced movement of ungulates poses even greater problems when two or more species are being handled. While remembering that reaction to handling is largely a function of previous training, it must be noted that threshold levels of response to stimuli and for onset of panic varies considerably among ungulate species (Hediger 1964, Ewbank 1968).

A level of handling stimulus appropriate to Hereford cattle may elicit alarm and panic responses in bison, for example. Panic is quite often contagious so that the emotion or behaviour in one animal spreads to others. A result may be that panic engendered in one particularly sensitive species is transferred to others.

Crowding

A distinction must first be made between chronic and acute crowding (Davis 1971). During acute stress there is a rapid neuro-hormonal response and then a return to average levels. In such circumstances sympathetic nervous stimulation leads to increased release of adrenalin and noradrenalin and an increased heart rate. This functions to increase chances of survival. However it is the condition of chronic crowding that is faced by most animals in captivity and under these circumstances the prolonged working of the General Adaptation Syndrome reduces an animal's chances of survival. Although resistance to the specific initiating stressor is enhanced, vulnerability to other potentially harmful stressors is increased.

Kiley (1975) describes chronic crowding as the central condition of intensive animal husbandry. Its behavioural and physiological effects on animals are beginning to be documented. How animals react to limited space depends largely on prior experience (Stokols 1972). Evidence seems to be (Stokols 1972) that lack of experience with density renders an animal more susceptible to crowding. In other words whether or not a given density is perceived as being 'crowded' depends on prior history of the participants. Previous population selection pressures may also be included as prior history.

It is evident that the condition referred to as crowding is in reality a complex interaction of several factors. Crowding constitutes an infringement on social and physical requirements, superimposed on an animal's prior history. As such, its causes and effects are many and varied.

Living space is a basic requirement of all animals, social or asocial. The area defining the living space is a compromise between the forces of approach and withdrawal (Kummer 1971, McBride 1972). Species typically existing in groups show strong approach tendencies. Within the social species, Hediger (1964) distinguishes between two extreme types of behaviour. These are contact species and distance species. Contact species (eg. many primates and rodents) deliberately seek contact with conspecifics during rest. On the other hand, the distance species (eg. most ungulates) maintain an individual distance (Conder 1949). Infringement of the individual distance is met with either withdrawal or aggression.

Admittedly, the organization of spacing behaviour is more complex than Hediger suggests. First of all, the personal field maintained is usually larger in front of the face than behind the animal (McBride 1972). Secondly, the extent of the individual distance controlled by each animal depends on its age-sex class membership and position in the social hierarchy. In addition, spacing distances vary depending on the nature of the activity in which the group

is engaged - whether it be resting, grazing or moving, etc. The result is a separate array of individual distances depending on the combination of the above factors.

Nevertheless, the likelihood remains that crowding and confinement seriously hampers the ability of ungulates to bring the spatial structure of their group into equilibrium. The immediate result of crowding is therefore to increase the level of agonistic encounters (Guhl 1969, Kiley 1974, 1975). Among bovids, increased aggression does not pose the danger that it does among swine and poultry (Kiley 1974); however frequent bunting may naturally result in injury to the bunted animal.

A second result of over-crowding is a change of social organization so as to alter the nature of the dominance hierarchy (Bryant 1972). At first signs of over-crowding, the hierarchy tends to become more rigid. Kiley (1974) points out that although a rigid hierarchy may initially reduce fighting, it also has the effect of preventing subordinate animals from approaching food or water troughs. With a further increase in crowding, even the rigid hierarchy breaks down and total organizational chaos results (Bryant 1972, Kiley 1974, Bareham 1975). It may be that in such conditions the animals do not have room to manoeuvre in such a way as to communicate through social posturing

Other effects of crowding such as reduced fertility and deficient maternal behaviour also have been documented

(Kilgour 1972, Kiley 1975).

Ethostasis

"Animals act on their environment not only in order to feed, drink, copulate, and avoid pain, but also to render a barren environment less monotonous, to gain access to social companions when housed in solitary confinement and to avoid extremes of temperature and illumination." (Fraser, et al. 1975)

During crowding or handling an increase in level of stressors is the problem, but during day-to-day maintenance, decreased stimulation has to be accomodated. Animals in the wild live in an adequately complex and stimulating environment. Although the husbandry of agricultural animals often involves stimulus-intensive situations such as handling and over-crowded housing, there is a trend toward reducing environmental complexity (Kiley-Worthington 1977). Fraser (1974) suggested that the term 'ethostatic' be used to describe those situations where restrictions of husbandry somehow impede normal activity. Ethostatic stress may be recognizable in many forms of abnormal behaviour among agricultural animals. Even when social companions are present, the monotonous environment may result in stereotyped behavicur sequences (Hediger 1964, 1965, Meyer-Holzapfel 1968, Kiley-Worthington 1977).

Stereotyped behaviour includes weaving, crib-biting (Kiley-Worthington 1977), pacing and complicated patterns such as playing with food or other objects (Morris 1964, Meyer-Holzapfel 1968). Fox (1968) describes such behaviour as being purposeless. He oversimplifies the situation. Animals may very well attempt to maintain an optimum range of environmental stimuli. If the level of stimulation falls below that range, animals may perform various 'abnormal and purposeless' actions in order to generate interaction with the external environment. In this sense, stereotypies should be viewed as adaptations to a particular environment.

CHAPTER FOUR

BEHAVIOUR IN CAPTIVITY - EXPERIMENTAL ANALYSIS

INTRODUCTION

Bison (*Bison bison*), Tibetan yak (*Bos grunniens*), and Hereford cattle (*Bos taurus*) are three bovids with quite different historical associations with man. These species were chosen for the study because they are being considered seriously for meat production from marginal lands in Alberta and because they provide a gradient of closeness of association with man. Bison and livestock unaccustomed to handling exhibit quite unlike responses when first exposed to handling. In groups of bison, panic can be induced relatively easily. To a lesser extent this is true of the yak. On the other hand, domestic stock show much less propensity for exaggerated responsiveness.

Species profiles

Hereford cattle (*Bos taurus*)

The Herefords were included to provide a reference permitting determination of the most important behavioural traits which may have changed during the process of domestication. The Hereford is a popular breed, well known to all North American and European cattle men. As much as

any breed, the Hereford has a long history of selective breeding. It is considered a docile manageable animal, well able to cope with intensive husbandry.

Tibetan yak (*Bos grunniens*)

The yak is native to the high regions of the Himalayas, usually not descending below 2400 m. above sea level (Epstein 1977). Principal breeders are the Sherpas, pastoralists who often migrate considerable distances with their yak herds every spring and fall. Domestic yak are loosely herded during the day and often tied or fenced at night. They have not undergone the intense selection for docility as Herefords have. Yak have been used for bullfights in parts of Asia and recently as rodeo stock in North America (Johansson 1978). Yet they are generally considered docile animals and reputedly make excellent pack and riding animals. Both zoologically, and in historical relationship with man, the yak occupies an intermediate position between the bison and domestic cattle.

Bison (*Bison bison*)

The North American bison has little or no history of selective breeding by man. In the spectrum of closeness of association with man, it represents the opposite extreme to that of Hereford cattle. Of the three species, only the bison is not of the genus *Bos* . However, some researchers (e.g. Bhambhani 1968), suggest that because of karyotypic

similarities that this native North American ungulate be reclassified Bos bison .

Except for brief attempts to tame bison for draft or beef production purposes during the nineteenth century (Roe 1972, Dary 1974) the species has not been kept in captivity on a large scale until the last 60-70 years. I have assumed that little significant genetic change can have been wrought on the population in so short a time.

It should also be noted that some testing included other ungulates available at the Experimental Farm. These were sheep, moose, wapiti, and Highland cattle.

Objectives

To attempt to gain experimental data dealing with the relative ability of 'wild' and domestic ungulates to cope with captivity, an eighteen month study was carried out at the University of Alberta Experimental Farm, Edmonton. The study was multifaceted in nature. It consisted of several experiments designed to evaluate the response of hand-reared domestic and non-domestic bovids to handling, and to identify other aspects of emotional make-up and interspecific relationships pertinent to animal management. Its focus was behavioural with physiological measurements being conducted only when they helped to identify levels of emotional response.

The study was designed to perform the following functions:

A. Evaluate the degree of habituation or increased sensitization of each species to routine handling

B. Appraise the three species studied and three other species with respect to basic levels of emotionality or 'temperament'

C. Document species inter-relationships and degree of diffusion of alarm reactions

D. Investigate effects of handling on performance factors (eg. feed intake and weight gain)

E. Suggest how management procedures may be modified to minimize stress related problems.

METHODS

A. Comparative Habituation to Handling

Calves of each species were removed from the range at age three weeks to one month. All calves were born on the range, either at the Athabasca Ranch, Hinton or at the University of Alberta Ranch, Kinsella. On the whole, early post-natal experiences of all animals were very similar. Calves were bottle fed at the University Experimental Farm until weaning. The experimental group consisted of 2 male Herefords, 2 female Herefords, 1 male bison and 2 female

bison. Considerable care was taken to control extrinsic environmental effects throughout the 18 months study period. All Hereford calves came from purebred Hereford stock owned by the Department of Animal Science. The yak used in this study were obtained from a herd owned by the Alberta Department of Agriculture. They descend from yak stock brought to Alberta in 1910 (Deakin et al. 1935). The bison I worked with were purchased from the Athabasca Ranch, Hinton, Alberta. Athabasca Ranch stock was bought from Elk Island National Park. No selective breeding has been practiced at either of these locations. Three female yaks were used. Of these, only one was taken at 3-4 weeks. The remaining two were abandoned by their dams and were therefore bottle fed from a much earlier age. Behavioural comparisons to these yaks were of only limited value since their early experience was different from the other experimental animals.

At approximately 5-7 months of age the bison and Hereford calves began on what was to be their routine schedule for roughly one year. Handling consisted of that necessary for a companion project on seasonal bioenergetics and adaptation to thermal environment. During the day, the animals were kept in a circa 500 square metre paddock. Twice a day the animals were individually fed, once a week they were weighed, and once a month put in a cold chamber for five to six hours during the day.

Throughout the experimental work, degree of habituation was evaluated by observations of behaviour. In an effort to standardize subjective judgements, a one to five scale was used when evaluating emotionality. When convenient, video tape recordings were used to record behaviour and assist in interpretation.

Subjective evaluations of behaviour and emotionality in wild and domestic ungulate species must take into account the fact that wild animals are usually quicker and more agile than domestics. This fact often results in misleading interpretations of temperament or emotionality. In attempting to further quantify these evaluations, tympanic membrane (ear drum) temperature was used as an index of emotionality. In brief, the rationale was that changes in blood flow during excitation are reflected as consistent changes in tympanic membrane temperature (Baldwin 1973). In the Bovidae, arterial flow is from the external carotid to the posterior auricular artery to the stylo-mastoid artery to the ear drum. As a result, ear drum temperature was expected to increase slightly with excitation.

A system devised by Howard Baldwin of the Alberta Fish and Wildlife Division and thought to be of potential value (Baldwin 1973) was tested during the study. Transmitters mounted on ear tags were equipped with temperature sensitive probes running to the ear drum. Problems in design and in mounting of the transmitters often prevented proper and reliable use of this technique. Nevertheless, some useful

data were recorded and it is my opinion that the system may still prove to be valuable in future evaluations of habituation and emotionality.

B. Temperament Tests

A series of tests originally designed as temperament tests for dogs (Murphree and Dykman 1965) was applied to ungulates of different background. Open-field behaviour, reaction to noise, to humans and to a dog were tested. Fourteen animals were used: 4 Herefords, 3 sheep, 2 bison, 2 yak, 2 moose, 1 wapiti. The sheep were of mixed-breed origin and were born on the University Farm. The moose were abandoned wild calves and were turned over to the Dept. of Animal Science at no more than 2-3 weeks of age. They were bottle raised at the University Farm. The wapiti was born on the Farm to a dam captured as an adult on the Ya-ha-tinda Ranch west of Sundre, Alberta. This calf was also bottle raised. Each test was performed twice, two days apart.

Open-field test:

Kilgour (1975) describes the open-field test as being applicable to the study of temperament in livestock. The characteristic measured is ambulation. However, various researchers have used high activity as an index of both high and low emotionality (Denenberg 1969, Kilgour 1975) As well, exploratory behaviour may be thought of as either related to or independent of emotionality (Whimbey and Denenberg 1967). In this test, I assume that a large number

of squares entered is indicative of high emotionality. Those species being tested typically run rather than freeze when frightened.

The animal to be tested was brought to a 45 sq. metre room. For two minutes each animal was observed from a one-way mirror as it moved about. The room was divided into squares, and the animals were scored on the number of new squares entered. The path of the animal was traced on a scaled drawing of the testing room. Vocalizations were also recorded. Data were analysed statistically by means of the Students' t-test.

Reaction to noise:

Through an opening from the observation room to the testing room, a loud air horn was sounded three times at fifteen second intervals. The animal's response was evaluated on a 1 to 4 scale ranging from little or no reaction to extreme startle reaction. The two-sample Median test, a non-parametric test able to handle ordinally scaled data (Siegel 1956), was used to determine differences in central tendency.

Social reactions to a neutral man:

An experimenter was seated at one corner of the testing room. A 2 meter radius circle was drawn around him. The time which the animal spent within the circle was recorded as long as the animal was attentive to the person seated.

Data were analyzed by the two-sample Median test.

Reactions to dog:

A fourth test was added to investigate the reaction of each animal to a predator stereotype - ie. a large domestic dog (husky-collie cross). Due to the danger of leaving dog and experimental animal alone in the testing room, I decided to remain in the room, with the dog on a two metre leash. Reaction was scored as one of four categories: (1) quick glances at dog but otherwise avoiding eye contact, (2) largely ignores dog, (3) orientation towards dog, (4) aggression towards dog. Categories were drawn up a posteriori, and were considered to represent a continuum from fear and avoidance to confidence and aggression. Data were analyzed by the two-sample Median test.

C. Species Interaction

In order to gain some understanding of inter-specific communication and social behaviour, several aspects of interaction were recorded. Spatial and social interactions were emphasized.

No single experiment was performed. Instead several kinds of interaction were recorded in order to gain an overall impression of the dynamics of inter-specific social organization and communication.

Nearest neighbor data while on pasture:

Observations were made over twenty days, records being taken with the animals resting and grazing. (scored on metric distance to nearest animal in a group of non-hand reared bison, yak and cattle)

Response to an isolated animal:

One subject from each species was separated from the group for a 30 minute period. (scored on degree of interest shown by members of each species in the separated animal)

Diffusion of alarm reactions during intensive handling:

Four tests were carried out twice each, to evaluate the response of one species to emotionaity in another. Each test used two species, one being handled so as to create alarm, the other to observe. Tympanic membrane temperature transmitters were working correctly for only two of the trials. They were chewed off by other animals, a persistent problem. (subjective evaluation + telemetrically monitored ear drum temperature)

Social rank:

A ranking was determined by displacements brought about by competition for restricted feed.

D. Effect of Handling on Feed Intake and Weight Gain

A second group of non hand reared bison, cattle and yak were given twice daily individual handling while feed intake

was monitored. A comparison was also made of weight gain in two groups of animals on identical ration but entirely different handling regimes.

Feed intake:

Bison, yak and Hereford cattle (two of each species) were kept in individual stalls for a period of 44 days. During this time the animals were fed consecutively, three different feeds.

Day 1-17: coarse timothy-alfalfa hay
Day 15-31: chopped grass hay
Day 28-44: pelleted alfalfa

Twice daily handling consisted of being weighed and moved around the barn for five minutes. Feed intake was recorded throughout the trial.

Weight gain:

A comparison was made of data arising from two similar studies of seasonal bioenergetics of bovids. The first trial took place during 1975-1976, and the second trial was the companion to the present study of 1976-1977. Rate of gain was calculated over a three month period in the fall for each group. As mentioned, ration was identical, but handling techniques differed greatly.

RESULTS AND DISCUSSION

A. Comparative Habituation to Handling

Initial responses (pre-weaning):

When approached for their first bottle feeding, all calves retreated and were obviously frightened. The first two to four feedings were forced. The calves would not voluntarily advance. After two to three days, however, all calves approached to feed. The Herefords milled about and pushed each other for the right to suck from the nipple bottle. Little remained of the original caution they once displayed.

Month old yak and bison retained their vigilance. They remained reluctant to approach. However, when they saw the milk bottle, they came voluntarily to drink. An obvious conflict existed between their reluctance to draw near to me and their desire to feed. The calves looked at the bottle and made sucking motions in the air, while standing roughly 2 m from me. Behaviour was frequently redirected to cross-suckling between the three bison calves. Usually, after 15 - 45 seconds of hesitation, the calves did advance and take the bottle.

Woolpy and Ginsburg (1967), working with canids, characterize four separate phases in the taming process: escape, avoidance, approach, and finally complete socialization. At the avoidance and approach stages they found animals to be very sensitive. Any actions that frightened an animal being tamed resulted in regression to an earlier phase, with further socialization then being very difficult.

The same obstacles were encountered at the University Experimental Farm. The bison remained somewhere between avoidance and approach stages. Any departure from the regime of gentle handling meant one-two days of avoidance behaviour. The bison were highly sensitive to all handling which was not routine.

As all calves became increasingly confident and familiar with the routine, the trauma that seemed to be associated with feeding diminished. Even the bison lost their initial hesitation. A distinct dissimilarity between the Herefords and the bison concerned routine. Any deviation from routine feeding procedures obviously upset the bison calves and they would retreat from the feeder. In addition, whereas the Herefords generalized their confidence with me to other handlers, the bison remained calm only in the presence of me (and one or two other familiar handlers). This observation has been corroborated at the Game Reserve of Western Canada (Miles and Beryl Smeeton, personal communication). Although the bison calves habituated rapidly to gentle handling the major differences remained: specificity of habituation to familiar handlers, and importance of routine.

Later handling (age 5-17 months):

Every week the animals were moved along a runway leading into a building where they were weighed.

Facilities in the building were entirely unsuited to the handling of large ungulates. A small weighing platform was surrounded by a barred fence less than one metre in height. The bison were easily capable of leaping over the railing. Nevertheless, as weighings became familiar, even the bison moved into the scale area without force having to be used.

Yet the bison remained always much more alert to the actions of the handlers than the Herefords. Their level of vigilance was rarely relaxed. Insofar as a decrease in vigilance is directly proportionate to the process of habituation (Mackworth 1969), the bison never truly habituated to forced, involuntary manipulation. Their generally high level of alertness and low threshold for panic reactions remained the distinguishing feature of the bison. Yet although the bison were always the first to show alarm in a stressful situation, they were also the first to approach familiar handlers in the field. The yak appeared to be more like the bison than Herefords with respect to level of alertness and specificity of habituation to familiar handlers.

When facilities are adequate, the bison's sensitive responsiveness can actually be used to speed up handling operations (personal observation, Elk Island National Park and Wood Buffalo National Park). However in our case, where escape response could be damaging to animals, equipment and handlers, it was imperative that all handling

stimuli be below that threshold. As pointed out earlier, the danger in handling mixed-species groups lies in the differing threshold levels. Techniques needed to keep Hereford cattle moving, for example, may be stressfull to bison. This was the situation faced at the University Experimental Farm.

During the course of 12 months of routine handling all animals adjusted well to non-forced movements. Entering stalls to be fed, or buildings to be weighed posed no problem. Yet unpleasant experiences such as remaining isolated in a cold chambre for 8 hours or being restrained in a cattle squeeze provoked trauma (continual attempts to escape, elevated respiratory rates), especially in the bison. Rather than habituation to these situations, the bison seemed to become increasingly sensitized. This behaviour in so far as it was undesirable, emotional and persistant, could be classified as neurotic (Fox 1968).

Stereotyped behaviour

Although causes are not well known, stereoptyed behaviour can be used as an index of environmental deficiency. It is difficult to evaluate the extent to which ethostatic stress affected the animals in this study. Daily handling and general activity around animal holding areas resulted in a relatively stimulus-rich environment. Nevertheless, stereotyped behaviour did

occur.

Crib-biting or pen-chewing appeared in all bovid species and also among wapiti kept at the research station. Many railings showed the effects of chewing, and some were almost gnawed through. Pacing was evident only in two cervid species, moose and wapiti. These animals, though hand reared, did not receive the same daily handling of the bison and cattle, and were kept in quiet, relatively little used areas of the experimental farm.

Cross-suckling of one calf on another turned up only in the bison and yak calves. The pattern continued until roughly 11 months of age in the bison and 13 months in the yak.

At the onset of the study, the assumption had been made that non-domestic species would be more easily stressed by inadequacies of the captive environment. Yet all species that were observed showed the development of some stereotyped patterns. A more detailed longer term study would be needed to determine with any certainty, variations in predisposition to suffer from environmental deficiency. As yet, no statement can be made to the the effect that the lower threshold level bison seem to display at high intensity stimulus levels holds for environmental deprivation.

B. Temperament Tests

The heterogenous group available for experimentation constituted considerable species and experiential diversity. In all, 14 animals were used: 3 sheep, 2 bison, 4 Herefords, 2 yaks, 2 moose, and 1 wapiti (Table 8). The grouping was not well suited to analysis of hereditary and environmental factors, yet one interesting dichotomy was available for comparative purposes: Domestic species (presupposed high stimulus threshold levels for emotional responses) vs. non-domestic species (low threshold levels).

Open-field test:

Dividing the data from experimental animals into 'genetically wild' and 'genetically domestic' produced no significant difference ($p \leq .05$) in number of squares entered by individuals of either group.

Reaction to noise:

wild ungulates are often assumed to react more violently to sudden noises than domestic animals. Results tend to confirm this suspicion. The 'wild' group exhibited a significantly greater level of startle response ($p \leq .05$) than the domestic species.

Social reactions to neutral man:

The two groups 'wild' and 'domestic', contained both hand reared and non hand reared individuals. It was hoped

TABLE 8. TEMPERAMENT TESTS.
Mean scores for each experimental animal

		OPEN-FIELD TEST (# squares entered)	REACTION TO NOISE (1 to 4 scale)	REACTION TO MAN (sec. in circle)	REACTION TO DOG (1 to 4 score)
Sheep	f	31	2.5	21	4
Sheep	f	79	1	38	4
Sheep	f	48	3	0	4
Bison	f	45	2	0	4
Bison	m	74	1	0	3.5
Hereford	f	28	3.5	0	3
Hereford	m	40	3	0	2
Hereford	m	38	3	0	2.5
Hereford	f	55	3	0	4
Yak	f	42	1	0	-
Yak	f	21	2.5	5	4
Moose	m	32	4	10	1.5
Moose	m	30	3	12	1
Wapiti	m	39	2	2	-

this test would help confirm whether there was or was not a remaining innate tendency for the non-domestic species to react differently tc human beings than the domestic. No

significant difference ($p \leq .05$) was found with respect to central tendency of the two samples. Here as well, a great deal of ambiguity surrounds the results. Time spent within the two metre circle may conceivably reflect either degree of socialization to humans, or exploration and investigation.

C. Species Interaction

Nearest-neighbour:

A second group of bison, yak and cattle were observed while on pasture. Social partnerships are at least in part a function of an animal's peer group during rearing (Pratt and Sackett 1969). Social partners (ungulates) may search for proximity while resting and even while grazing (Bouissou and Hovels 1976). Each species had been raised with conspecifics only until 8 months of age. As a result, expectations had been that each animal would associate more with its own species counterpart than with individuals of other species, but results indicate that this was not the case (Figure 7). The bison, for example, were more often found in association with yak and cattle than with each other.

Response to isolated animal:

A female bison was put in an adjacent paddock apart

Nearest-Neighbour

	Bison	Yak	Hereford	Highland
Highland	15.6 (25)	11.9 (19)	13.1 (21)	2.5 (4)
Hereford	18.8 (30)	7.5 (12)	6.3 (10)	
Yak	10.6 (17)	10.6 (17)		
Bison	3.1 (5)			

% Occurence of Nearest-Neighbour {Metric Distance Between Individuals}
Actual Frequencies in Parentheses

Based on 20 Observation Days from May 22 to July 21, 1976

Figure 7. Percentage occurence of nearest-neighbour -measured as distance between members of four species/breed groups while in a circa 100m X 50m pasture. Actual frequencies are given in parentheses.

from the yak, cattle and the other bison which constituted her peer group. Such a situation, where an individual is isolated from its conspecifics is, for ungulates, a very effective stimulus to vocalize (Kiley 1972). The separated bison vocalized for approximately nine minutes. Answering vocalizations were elicited only from the one other bison, the male. The rest of the animals showed only a fleeting interest. On the other hand, the male bison stayed close to the fence separating the two animals and they frequently called to each other. After roughly 10 minutes the male stopped all vocalizations, but remained near the female for the rest of the 30 minute separation period.

A female Hereford was similarly separated for 30 minutes. The isolation evoked no more than 2 minutes of vocalization. No answering calls came from either her conspecifics or bison or yak. Only the female bison remained near the separating fence. After 7 minutes, she wandered farther away, but was still the only animal that remained near by.

The strength of bonds between conspecifics seemed much more firmly established among the bison than the cattle. This trait is evident in the response each bison showed to isolated members of its peer group, wether they were Herefords or bison.

Social hierarchy:

Figures 8 and 9 depict the dominance hierarchy at age

2-4 months and at 17-19 months respectively. I thought that one species might consistently dominate another. A result of such a situation could be that one species would regularly deprive another of access to feed troughs as has been found in groups of cattle (Wagnon 1965).

No such simple alignment of dominance was found to exist. There was no evidence of division into alpha species, beta species, etc. as predicted by Hediger (1955).

The ranking at age 2-4 months (before puberty) did not remain unchanged. Comparison of Fig. 8 and 9 shows that there was more ambivalence in the social hierarchy at 2-4 months than at 17-19 months of age. The bison male, probably due to his weight disadvantage with respect to the Herefords, lost his place atop the hierarchy.

Bouissou (1972, 1977a) is one who has suggested that for domestic cattle, dominance relations may be predicted largely on the basis of body weight, presence of horns and age/experience factors. In this mixed species group as well, social rank seemed closely related to body weight (Figure 10). The age/experience variable was roughly equal for all individuals

The Herefords were de-horned at birth whereas the bison and yak had horns. Yaks possess very large impressive horns. It is possible that mature yaks, despite their smaller size, may have some competitive advantage over bison and cattle because of their large horns.

Dominance Hierarchy
August-September 1976

Losers

Winners

	1140	45	1142	40	46	47	1141	1145	1144	1146	Total Wins
1140		3	7	10	7	2	14	5	1		49
45	2		2	1	4	3	3	3			18
1142	3	2		7	4	4	10	5	4	2	41
40	1	2	4		3	9	4	3	5	2	33
46		2	2			3	3	1	3	4	18
47					1		2	2	5	5	16
1141					1	2			4	5	12
1145									20	14	34
1144										12	12
1146									7		7
Total Losses	6	9	15	19	20	23	36	19	49	44	240

40	♀	Hereford	1141	♀	Bison
45	♂	Hereford	1142	♀	Bison
46	♂	Hereford	1144	♀	Yak
47	♀	Hereford	1145	♀	Yak
1140	♂	Bison	1146	♀	Yak

Figure 8. Ranking of bison, yak and Hereford cattle based largely on competition for restricted feed. All animals aged 2 - 4 months.

Dominance Hierarchy
- January 1978

Losers

Winners

	45	46	1140	40	1141	1145	47	1144	Total Wins
45		3	5	2	1	6	4	3	24
46	1		3	2	3	7	2	2	20
1140		1		6	5	5	1	2	20
40	1				2	11	2	9	25
1141						6	4	9	19
1145	1				1		4	3	9
47						1		2	3
1144					1		2		3
Total Losses	3	4	8	10	13	36	19	30	123

1140 ♂Bison
1141 ♀Bison
1144 ♀Yak
1145 ♀Yak

40 ♀Hereford
45 ♂Hereford
46 ♂Hereford
47 ♀Hereford

Figure 9. Ranking of bison, yak and Hereford cattle based largely on competition for restricted feed. All animals aged 17 - 19 months.

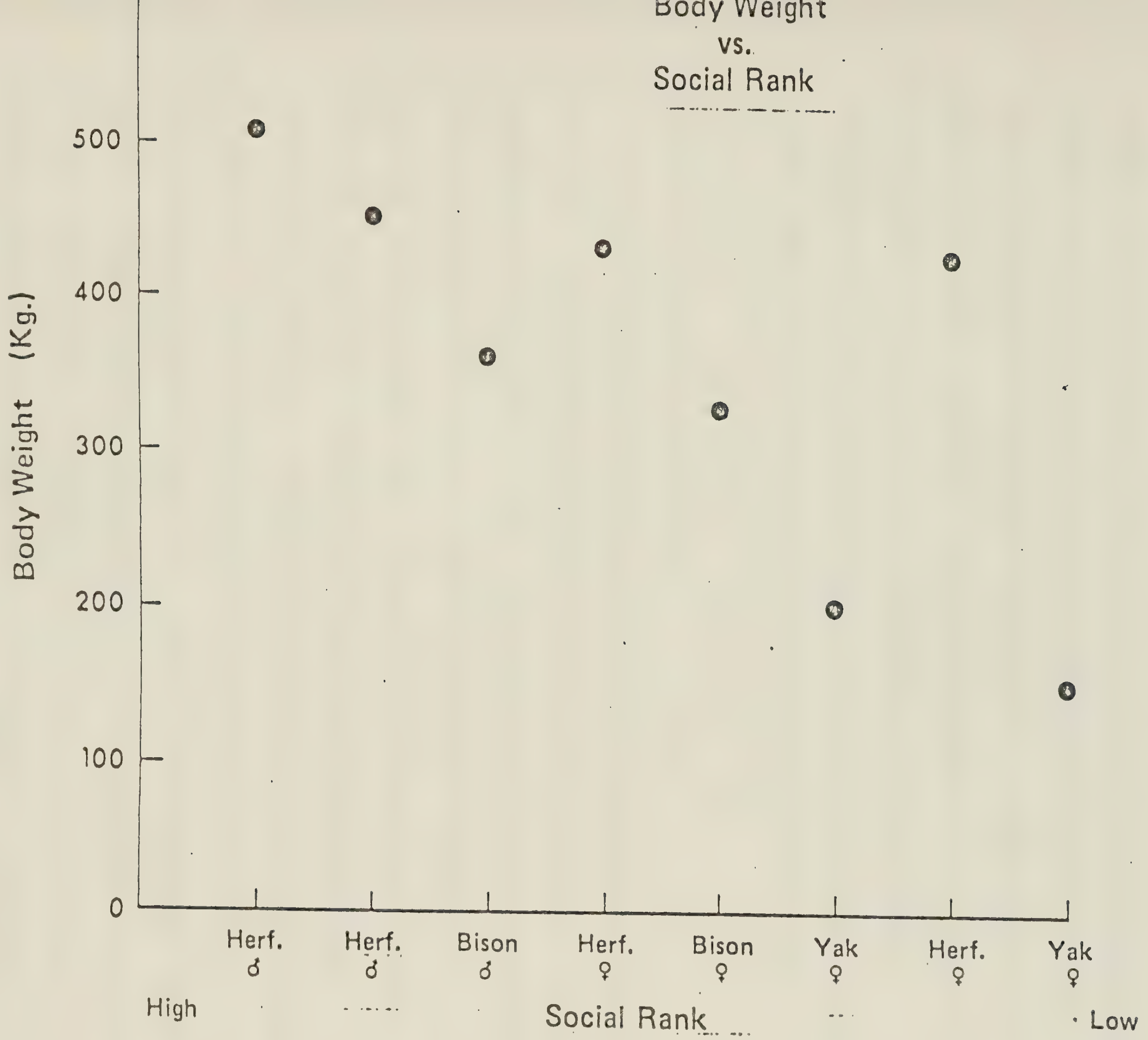


Figure 10. The relationship between body weight and social rank in a group of 18 month old bison, yak and cattle.

The implications of these findings are that mixed species groups in all likelihood would not result in one or two of the species being excluded from access to resources such as feed and water. Yet it would be wrong to generalize the results obtained here to all bison-yak-cattle interaction. In cases where the animals have not been raised together but instead brought into contact first as adults, a quite different interaction pattern may arise. The results of initial agonistic competition may be generalized to all members of the competing species thereby giving rise to an actual biological ranking of species.

Diffusion of alarm reaction:

In most species of ungulates, when behavioural signs of alarm are expressed by one individual, alarm quickly spreads throughout the group. This is well-known to any herdsman, who knows that successful animal handling depends on avoiding panic reactions. Range cow milking operations at the University of Alberta Ranch (personal observation) demonstrate well the effect of diffusion of alarm and panic responses. Sixty-five cows were milked daily by being run into a cattle squeeze one at a time. Periodically, cows became alarmed while being milked. Vocalizations from the stressed individual resulted in all other cows within hearing distance being much more difficult to move along the runways to the squeeze. The question being posed here is: Can such alarm reactions readily cross species barriers?

Four tests were carried out twice each, to evaluate the response of one species to emotionality in another. Each test used two species, one being handled so as to create alarm, the other to observe.

1) Herefords observing bison: The lower threshold for bison alarm reactions were thought to be a potential trouble area in handling the bison-cattle group. In addition to the bison themselves being difficult to handle in a panic state, I thought the Herefords might also become upset thereby making any handling more difficult.

Herefords gave no visible signs of upset except attention to the movement of bison and handlers. When the Herefords' paddock was entered, they moved away from handlers, allowing approach only to within 2 metres. Normally, these same animals could be approached and touched. During the second run of this test ear drum temperature transmitters were functioning. The ear drum temperature of the bison heifer was elevated and fluctuated considerably during the most severe handling (Figure 11). No comparable fluctuation was found in the Hereford observer. Even when the Hereford was handled roughly, tympanic membrane temperature fluctuations never approached those of the bison (Figure 12).

2) Yak observing bison: Yak displayed obvious interest in the bison handling. The yak would follow the movement, running along with tail carried high, as far as the

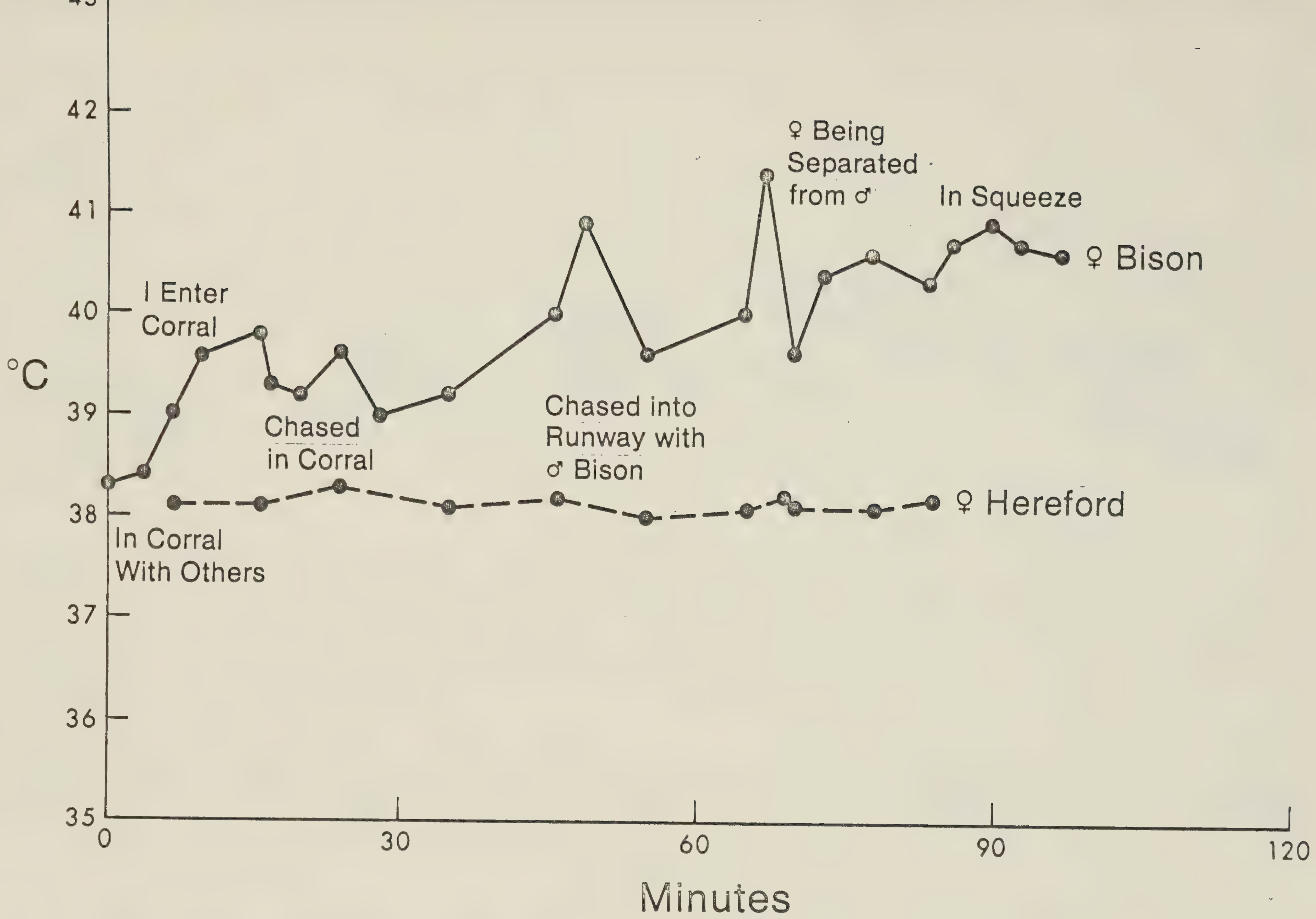


Figure 11. Changes in ear drum temperature of a female bison during handling. The broken line represents the ear drum temperature of a female Hereford watching the handling of the bison.

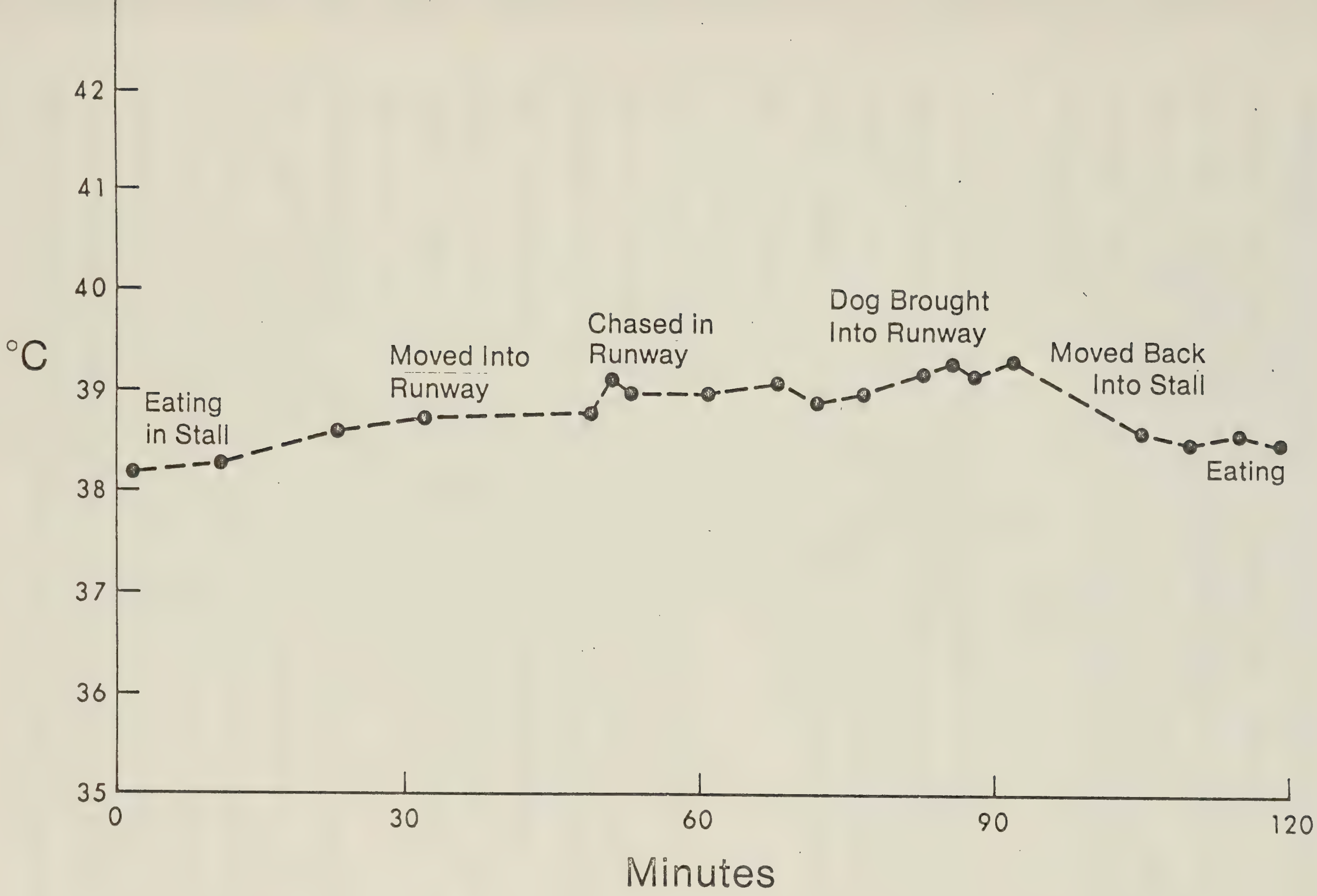


Figure 12. Changes in the ear drum temperature of a female Hereford during handling.

restrictions of their pens would allow. When their pen was entered, they would not allow handlers to come near. Normally the yak would allow handlers to come within one metre and would then themselves initiate contact. Their attitude towards handlers had clearly been changed by what had taken place.

3) Bison observing Herefords: With the cattle being run at high speed, no visible signs of stress were displayed by the bison. However, when the bison were later approached, they would withdraw . Again it seemed the observing species had been frightened.

4) Herefords observing Herefords: Reaction of cattle watching conspecifics being run was no different than that recorded after watching bison. Again no visible signs of emotionality were discernible, yet the animals showed an elevated level of nervousness when approached a few minutes later. Figure 11 illustrates the fluctuation in ear drum temperature correlated with harsh handling. The differences in the temperature response curves of Herefords and bison is considerable, and may be interpreted as evidence of a difference in emotionality during handling.

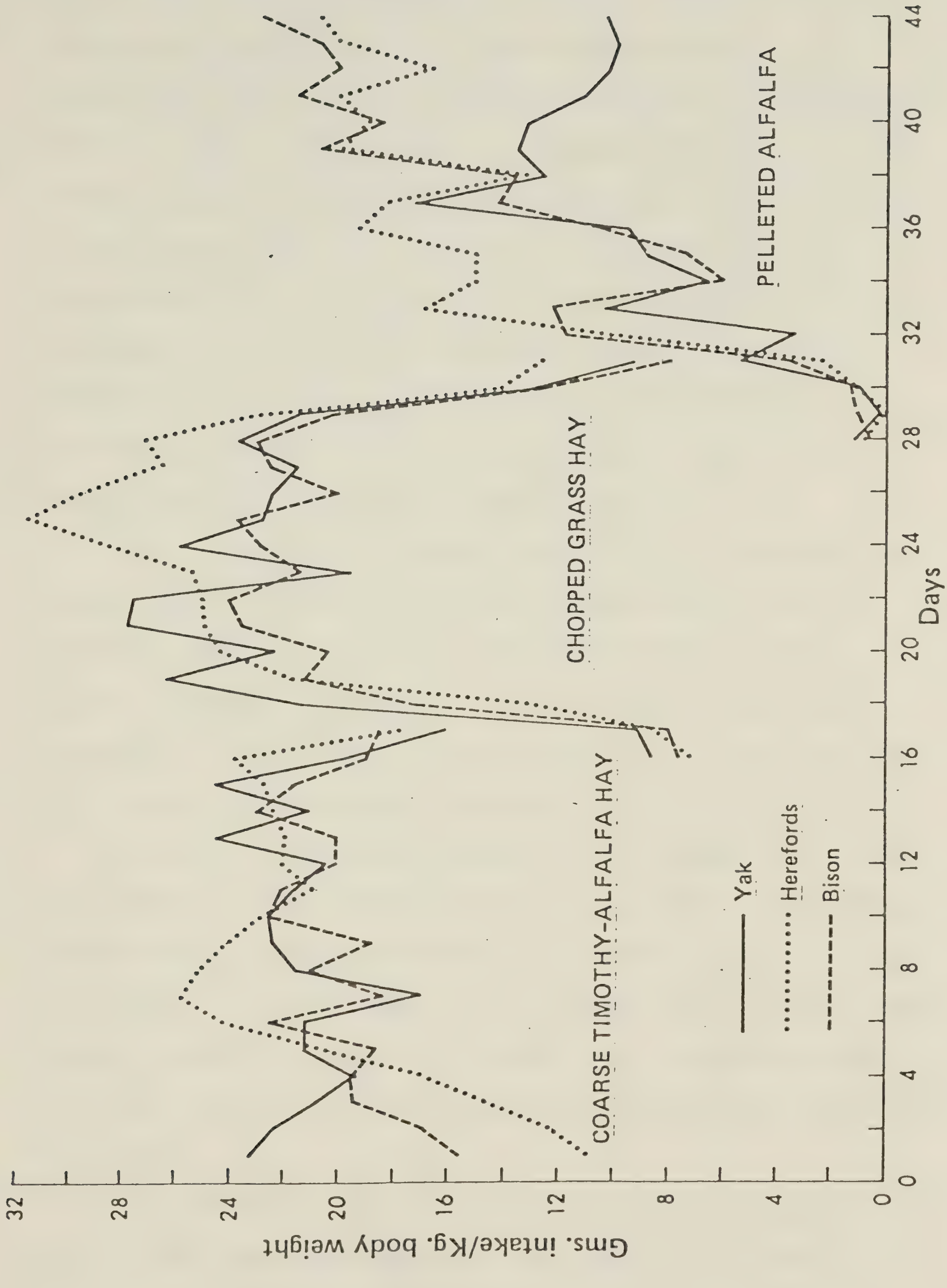
The tests described above do not prove or disprove true recognition by one species of emotionality in another. Yet it can be stated firmly that all species did react to some degree to the visible and audible signs of alarm in another,

though responses of Herefords were milder. Secondly, it seems, at least in the case of the Herefords, that reaction to alarm of conspecifics and of bison is no different.

D. Effects of Handling on Feed Intake and Weight Gain

Most domestic animals are herbivores with flexible diets. Domestic cattle have been selected for high rate of gain and therefore, in effect, for increased appetite, reduced selectivity and docile temperament (Tulloh 1961b). Figure 13 graphs the feed intake of bison, yak and cattle over a 44 day period. As expected, Herefords averaged a somewhat higher level of feed intake. Response of each species to new feed was very similar. The feed intake within each conspecific pair was quite consistent, with one exception. The considerable reduction in intake shown by yak beginning on day 35 was due to one animal only. Initial differences in intake of the first ration (coarse timothy-alfalfa hay) may have been due to variation in feeding before the trial began. A two-day overlap was allowed at each change of feed. Response of each species to new feed was similar. There appeared to be some reluctance to change from familiar to unfamiliar rations. This was most clearly apparent at the change to pelleted alfalfa. It should be noted that the second ration (brome-grass hay), may have been the most palatable. As a reaction to handling, I had assumed that bison would 'go off' feed to a considerable extent, at least compared to cattle. No such response was

FIGURE 13. Yak, Herefords and bison (two of each species) were fed three different feedstuffs, and were handled twice daily. Feed intake was monitored as a response to (a) novelty of feed and (b) handling stresses.


Gms. intake/Kg. body weight
32
28
24
20
16
12
8
4
0
0
4
8
12
16
20
24
28
32
36
40
44
Days
COARSE TIMOTHY-ALFALFA HAY
CHOPPED GRASS HAY
PELLETED ALFALFA
Yak
Herefords
Bison

found, and it may be that each animal had habituated to everyday farm handling by the time of the trial. All animals had been obtained 16 months previously at roughly 8 months of age. Bison (and to a lesser extent the yak) seemed to react to daily handling with a much higher level of nervousness than the cattle. Bison easily became panicked and kept maximum distance from handlers. On the other hand, Herefords were extremely docile, and it was difficult to initiate walking. Perhaps the bison, accustomed to some handling, regained their composure quickly thereby not affecting feed intake.

Table 9 shows considerable variation, as reflected in average daily weight gain, between animals subjected to different handling regimes. Both groups were used in similar metabolic research. For all animals, handling consisted of weekly weighings and monthly periods spent in a cold temperature metabolic chambre.

The major difference between the two groups lay in that all handling of the '75-76 group was done by animals being individually haltered and coaxed or forcibly pulled to their destination. On the other hand, during '76-77 animals were usually moved in groups of at least two. Emphasis during '76-77 was on establishing routine and minimizing stressful experience.

The premise is that the former handling system was considerably more stressfull to the animals involved. I also assumed that an animal's performance is the integral

Average Daily Gain Over 3 Month Winter Feeding Period
1975-76 vs. 1976-77

(kg/day)

Species	1975-76	1976-77
Hereford	0.710	0.806
Bison	0.421	0.546
Yak	0.112	0.408

TABLE 9. AVERAGE DAILY GAIN OVER A THREE MONTH WINTER FEEDING PERIOD.

A comparison of the effects of two different handling systems on weight gain. Members of the 1975-76 group were haltered and handled individually. During 1976-77, on the other hand, animals were moved about in groups and every effort was made to minimize handling related stress.

effect of all ambient factors (Wilson 1971) and that as a result, the energy requirements of a nervous animal are disproportionately high (Tulloh 1961b, Geist 1971). It may be, therefore, even though the experience of emotional stress and hypervigilance does not reveal itself as reduced feed intake, that less of the potential energy value of the feed is available for growth in a nervous animal. Tulloh (1961b) found that docile animals grow more quickly than animals which are restless, nervous or aggressive. He concluded that the effect of selecting for animals based on live weight gain is to simultaneously select for ones with good temperament (defined as how quiet the animal is in confined, restricted quarters).

CONCLUSION

What conclusions can be drawn from these numerous pieces of observation and experimentation? No single test or observation alone describes the differences in responsiveness of domestic and non-domestic ungulates, and little evidence has been presented regarding the range of variation between these two groups. It may be more proper to say that the collective evidence suggests few absolute differences exist between domestic and non-domestic. Comparing bison and Hereford cattle, the interesting result is that qualitative differences are so few. In many of the behavioural tests and tests concerning handling, little or

no difference was found: e.g. open-field, response to predator-type, social reactions to human, nearest neighbour, diffusion of alarm reactions, new feedstuff acceptance, handling and feed intake.

How did the bison and cattle groups differ?

1) Bison retained a much higher level of alertness to any visual or audible stimuli.

2) Maintaining the routine of handling remained more important to bison than to the cattle.

3) Bison did not generalize their confidence with familiar handlers to other people to the same extent the cattle did.

4) Peer group bonds appeared to be stronger among bison than cattle.

The working hypothesis has been that much of the difference in responsiveness between wild and domestic ungulates can be attributed to unlike stimulus-response thresholds. Where differences did show up, perhaps they also can be interpreted within this framework. As a group, for example, non-domestic species showed a greater startle response to loud sound than the domestics.

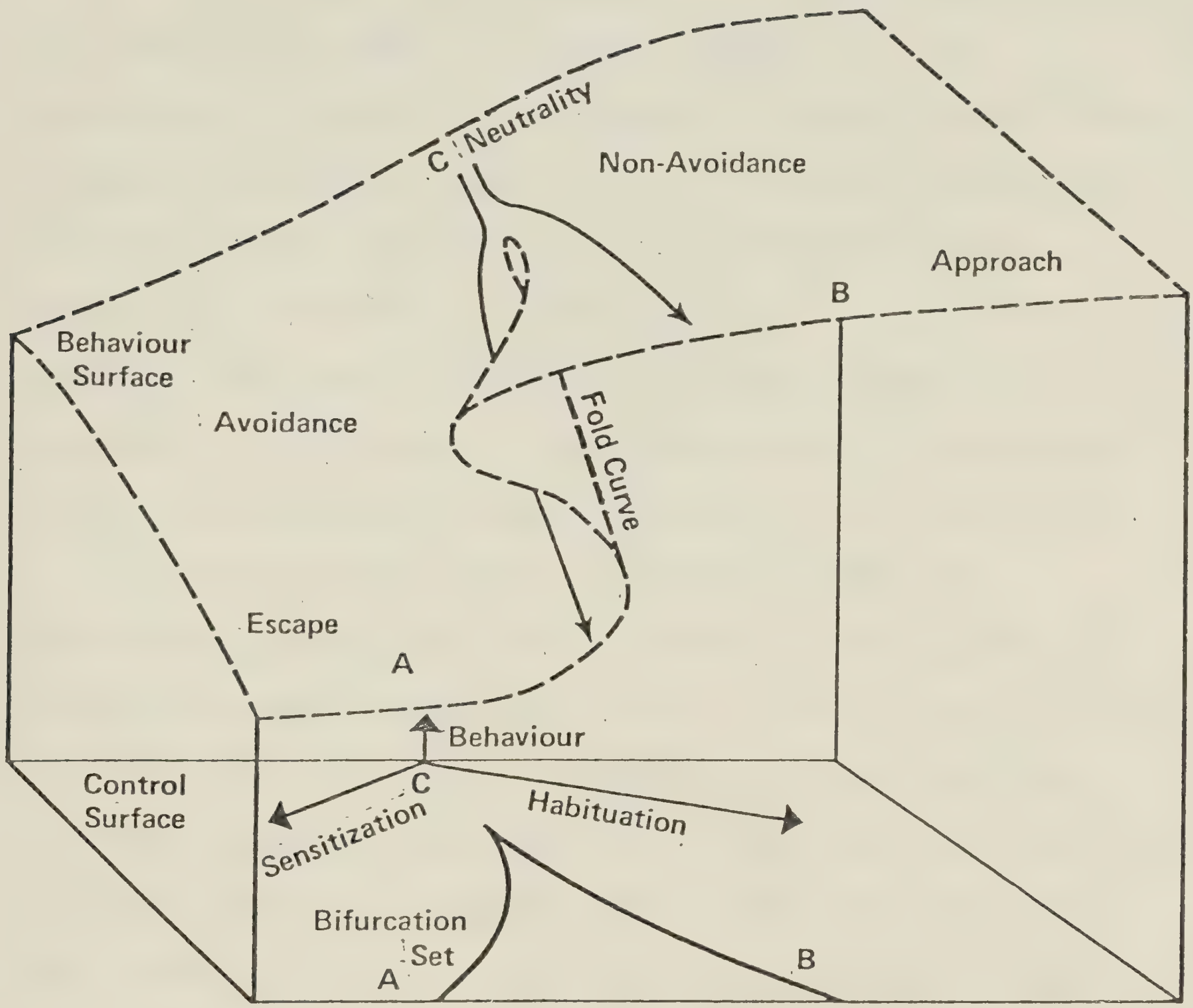
More interesting from a practical standpoint, are the data concerning the relation between management system and weight gain. These results indicate that variation in management techniques may in fact produce significant differences in performance variables such as weight gain. As mentioned previously, it has been sugested that when

animals are stressed and nervous, their physiological energy requirements become elevated (e.g. Tulloh 1969b, Geist 1971). This seemed to have been true for all three bovid species. Findings such as these re-emphasize the importance of adopting handling techniques that minimize emotional stress.

Based on the information accumulated, it seems inappropriate to generalize and categorize the responses of one species. Habituating the bison to handling was a more delicate process and took more time than with the Herefords. Because their habituation to people was highly specific and any deviation from routine quickly noted, they were capable of rapid changes in their reactions. The impression is that the early background of the animals and the handling system being used are as important determinants of emotional response as any species-specific tendencies.

Two models of behavioural response

Figures 14 and 15 are topographical models representing animal responses and the factors influencing those responses. Catastrophe Theory (Figure 14) is described by Zeeman (1976) as being applicable to those situations where "gradually changing forces lead to abrupt changes in behaviour." It has been adapted here to illustrate how any gradual movement of an animal along the sensitization-habituation axis (control surface) may precipitate 'catastrophic' changes in behavioural responses (behaviour



Catastrophe Theory

Response to Handling

Habituation Process Leads to Tameness
Sensitization Process Leads to Exaggerated Avodiance and Neurosis

Figure 14. A topographic model designed to show how a slight change in terms of sensitization-habituation (control surface) can result in a dramatic change in behavioural response (behaviour surface).

surface). The model becomes particularly useful in describing the critical approach and avoidance phases of the taming/socialization process (e.g. Woolpy and Ginsburg 1967). Any slight regression from position B to position A will result in a return to escape responses. As illustrated in Figure 14, increased sensitization may lead to abrupt changes in behaviour. For example, during rearing of bison calves, rapid habituation to feeding routine resulted in approach to handlers (position B in Figure 14). Departure from routine lead to a somewhat higher level of alertness (i.e. increased sensitization and a considerable change in behavioural response (position A in Figure 14).

The second model (Figure 15) illustrates the interactive effects of stimulus intensity and spacing on emotional arousal (Henderson 1969). The left hand side of the model shows elevated emotionality. In veterinary ethology terms, this would be due to ethostatic stress. On the other hand, the response peak at the far right corner would be caused by continued high-intensity handling.

The general pattern of the emotional arousal surface is probably similar for most ungulates. Differences may be in that response peaks and gradient slopes will be greater in most wild as compared to domestic ungulates. In ungulates newly brought in from the wild, the whole of the emotional arousal surface is considerably elevated. The process of habituation consists of lowering this surface to where an optimum combination of handling intensity and spacing will

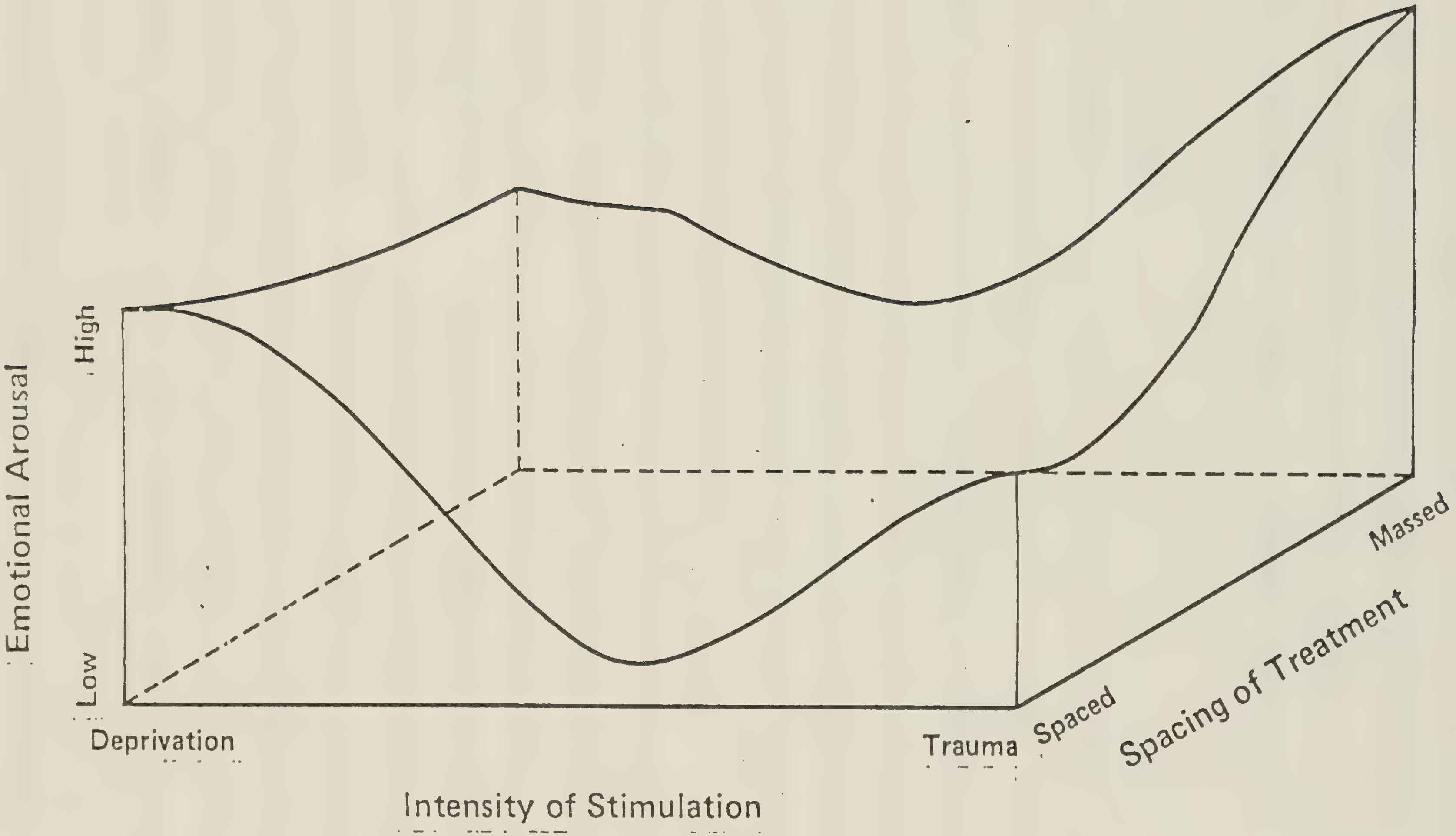


Figure 15. A topographic model illustrating the inter-related effects of stimulus intensity and treatment spacing on emotional arousal. (Henderson 1969)

result in an acceptable level of emotionality. Both models reflect and sum-up the assumptions I make in this study. The models show that previous training and experience as well as variation in the immediate circumstances can work together as complex modifiers of actual responses.

Handling guidelines

The argument I am making, of course, is that there is no ONE handling technique appropriate to bison, another to yak, and another to cattle. Although in general, handling techniques for one species may not be good for another, I suggest, because of the importance of early experience to later behaviour, that management systems must as well be fitted to individual circumstances.

A part of this study consisted of hand-raising related bovid species from age 3-4 weeks. The results obtained are applicable to other bison, yak and Hereford cattle tamed from a similar age. However, they CANNOT be generalized completely to predict the reactions of, for example, animals imprinted to man from birth, or brought into captivity as adults. Some generaliztions can be made, and have already been stated. They concern group cohesion, specificity of habituation, general level of alertness, and the importance of routine.

Intensive husbandry may not be the economically most viable level at which to manage bison. Extensive mixed-species grazing systems with a low level of management are

probably better suited to marginal lands livestock production.

What has been shown here is that bison are not incompatible with intensive husbandry as long as handlers are aware of some principles of animal behaviour. Because they are very sensitive to their surroundings, bison may actually be easier to manipulate in some ways than Hereford cattle.

CHAPTER FIVE

REACTIONS OF BISON TO HANDLING DURING A VACCINATION PROGRAM IN WOOD BUFFALO NATIONAL PARK

Introduction

In the previous chapter I discussed the results of behavioural research carried out on small groups of animals. I suggested that an understanding of the factors influencing animal behaviour is imperative in order to optimize housing and handling techniques.

Presented here is an ethological analysis of a large-scale bison handling program. Its intent was primarily to provide a guide by which the Park Warden Service could reduce handling related mortalities and injuries. Reports of results and recommendations have already been presented to Parks Canada (Hudson, Tennessen and Sturko 1976, Tennessen and Hudson 1977).

Wood Buffalo National Park contains one of the largest herds of wild bison in the world. The wood bison (*Bison bison athabascae*) was the original inhabitant of the region. However, between 1925 and 1928, over 6000 plains bison (*Bison bison bison*) were introduced from Wainwright, Alberta. Most animals presently within the Park are

believed to be hybrids. The rate of population increase is not known with certainty because of variation in the census techniques. The bison population reached a high of about 12,000-15,000 around 1940. Since then herds have been depleted by disease, poor weather and spring floods to the present level of roughly 6500 bison.

In 1964 an outbreak of anthrax occured among the bison herds of Wood Buffalo National Park and attempts were made to remove infected herds. Since that time, periodic roundups have been held to vaccinate segments of the population.

Roundups represent stressful experiences for bison, and Park managers have been concerned because the roundups have resulted in some animal mortality. In addition to those stemming from physical injuries inflicted in the handling chutes, losses of animals during long drives to holding corrals and subsequent to vaccination have been documented.

Stress, such as that experienced by bison during vaccination programs, has numerous manifestations some of which are apparent at the time of disturbance and others which may not be evident for days or even weeks later. Immediate results include intense crowding, social disorganization, breakup of cow-calf units, redirected aggression, frantic attempts to escape, and fear induced immobility.

Physiological manifestations of stress are numerous. Perhaps the most serious disorder is one termed capture myopathy or overstraining disease. Capture myopathy is also most interesting from a behavioural point of view since its occurrence is evidence of physiological and/or psychological stress (Basson and Hofmeyr 1975). The disease may occur within 1 day to 4 weeks after handling, but usually appears within 1 to 2 weeks (Basson and Hofmeyr 1975). Affected animals show pain, stiffness and muscular dysfunction. Some animals may die suddenly from acute heart failure without showing prior symptoms. Muscular lesions are found in the limbs, back and often the heart. Affected muscles show lighter greyish brown portions which are often striated in appearance.

METHODS

The work described was conducted during two successive anthrax vaccination roundups, June 1976 and June 1977. Bison were rounded up by helicopter and driven up to 20 km. to holding pastures at Sweetgrass Meadows (see Figure 16). Observations were made of the animals as they were brought towards the handling facilities and periodically in the holding pasture during the day.

The next morning vaccination began. Groups of 100-200 animals were separated from the main herd by a bombardier tracked vehicle and driven to a capture corral. Here the

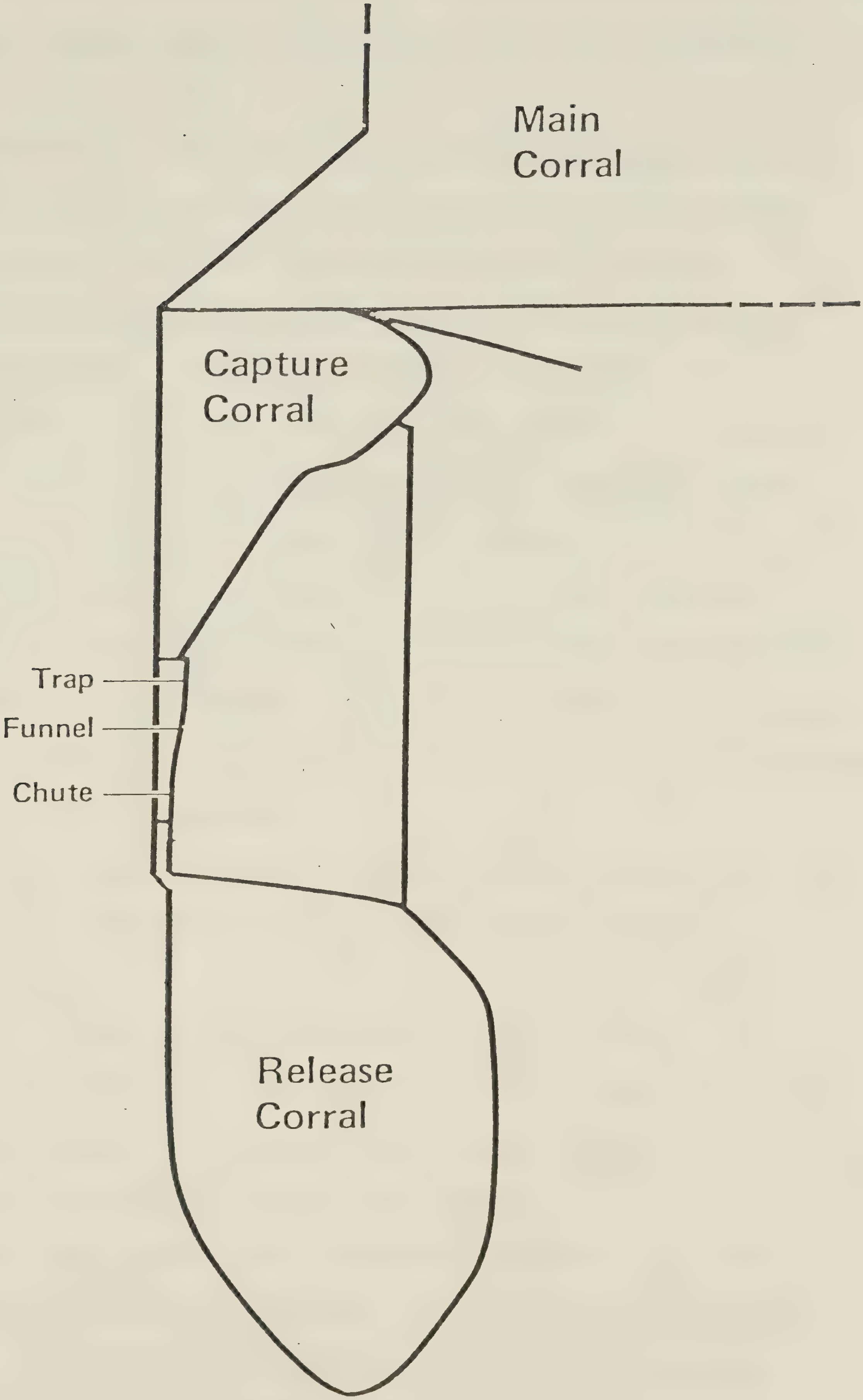


Figure 16. Bison handling corrals at Sweetgrass Meadows, Wood Buffalo National Park

herd was again subdivided and 20-80 animals were driven into a funnel shaped trap at the entrance to the vaccination chutes.

Analysis of the effects of handling procedures were made at several points. The main site for behavioural analysis was the funnel where animals were kept in relatively crowded conditions and in close proximity to human handlers. Emotional tension and unrest were interpreted by the level of agonistic behaviour and by the degree to which dispersion of the group remained stable. Observations were also made during herding by the bombardier, in the chutes and in the holding pasture. Videotape recordings of bison behaviour were made whenever possible. Physiological measurements, consisting of rectal temperatures and respiratory rates, were taken in the chutes throughout the operation.

Longer term effects of handling were assessed by holding the final bison to be processed in the main corral.

1976: 115 bison were held for 2 days.

1977: 124 bison were held for 7 days.

The herd was watched daily for signs of capture myopathy and for cows returning to claim lost calves.

The report submitted to Parks Canada of the 1976 vaccination (Hudson, Tennessen, and Sturko 1976) made a number of recommendations for improvement of handling procedures. Many of these recommendations were implemented

in 1977.

RESULTS AND DISCUSSION

Physical Injuries

A detailed breakdown of fatal injuries sustained during the vaccination program is given in Table 10. The funnel area was the most dangerous one for the animals.

TABLE 10. INCIDENCE OF FATAL INJURIES.
Percentage values corrected for abundance of each age/sex class in parentheses.

	Calves N=227	Subadults N=205	Cows N=887	Bulls N=432	Total N=1751
Main Corral	-	1(.5)	1(.1)	-	2(.1)
Capture Corral	1(.4)	-	-	-	1(<.1)
Trap	-	2(1.0)	1(.1)	1(.2)	4(.2)
Funnel	1(.4)	9(4.4)	4(.5)	-	14(.8)
Chute	-	2(1.0)	1(.1)	-	3(.2)
Release Corral	1(.4)	-	-	-	1(<.1)
TOTAL	3(1.3)	14(6.8)	7(.8)	1(.2)	25(1.4)

Nevertheless, the number of fatal injuries was not high, accounting for 1.65% of the herd in 1976 and 1.11% in 1977. The funnel was associated with extreme psychological and physical stressors. Subadults (yearlings and two year olds of both sexes) and mature cows accounted for most of these losses (Table 10). Subadults were exposed to by far the greatest risk (Table 10). Subadults may be the common victim due to their low social status within the herd.

TABLE 11 AGONISTIC INTERACTION AMONG BISON IN THE FUNNEL. Sweetgrass Corrals, 1976 & 1977.

ATTACKER	ATTACKED			
	Bulls	Cows	Subadults	Calves
Bulls	.93(35)	.49(38)	3.65(65)	.71(14)
Cows	.14(3)	.55(25)	4.99(52)	.78(9)
Subadults	-	.15(2)	5.69(18)	2.00(7)
Calves	-	-	-	-

Chi-square: Significant at .05 level of confidence

Values = observed frequencies divided by expected frequencies based on herd composition. Actual values in parentheses.

When the bison were first chased into the trap there was a tremendous amount of jostling as they piled up at one end. Occasionally the animals were crushed together so severely that some were lifted above the the rest. A cow found dead the day after the 1977 vaccination probably sustained her injuries during this initial crush.

Goring and trampling were also major causes of injuries in the funnel. Large bulls were especially dangerous when the animals were crowded together. In two instances, herding of the animals by the bombardier led to injuries. In the confusion created by high-speed chase and the bison trying to escape, a young female ran into the side of the machine, and a calf was trampled.

Psychological Stressors

For the bison, there is undoubtedly a good deal of fear associated with capture and handling. The pursuit by helicopter and bombardier, the crowding, and the close presence of humans all contributed towards psychological stress.

It is the emotional tension experienced by bison in the funnel that in large part makes it such a dangerous area. Here the bison are faced with the dilemma of either dispersing, thereby approaching the handlers visible on the catwalks, or crowding together, infringing on the personal space of other animals. Violation of personal space

usually results in agonistic behaviour, with subordinate animals suffering (Table 11). Large bulls maintain large individual distances between themselves and the next animal.

A general recounting of actual attacks by one animal on another gives an oversimplified picture of agonistic behaviour. Nod-threats and other subtle interactions not easily discernible by an observer (Lott 1974) add to total emotional stress.

Both years, the bison group responded to the dual pressures by alternately dispersing to fill the funnel area and then compressing into a small space. The bison were never able to completely relax but rather fluctuated between one stressful situation and another.

Separation of Cows and Calves

The use of a high-speed tracked vehicle to cut groups of bison off from the main herd resulted in panic and confusion among the animals. As some animals splintered off, cows and their calves were often separated. During the 1976 vaccination, it was standard procedure to let the bison free in small groups. If cows and calves both returned to the place they were last together, this separation would be a minor problem. However, although the calves returned to the handling facilities, only a few cows did.

The morning after the 1976 operation, 19 calves and two yearlings had collected in and around the labyrinthine corral system. For the next 2 days gates were opened periodically to allow them access to the sample of 115 bison. 8 calves appeared to have successfully paired with cows from this group. Abandoned calves seemed to take the initiative in regaining contact.

It was surprising that most cows either did not actively search for their calves or did not dare approach the corral system. Presumably the process of being vaccinated was so traumatic for the adult animals that the tendency to return was not strong enough to overcome their fear of returning to the site of their earlier stressful experience.

A recommedation of 1976 was, therefore, that after leaving the chutes the animals should be kept behind in the release corral. This would allow for more cow-calf units to be re-established before release. Accordingly, only three large group releases were made in 1977.

In 1976, 14% of calves were found to have been separated from their dams. In 1977 that number was reduced to 7%.

These figures may be conservative. It is conceivable that other calves may have been carried along for such a distance by the fleeing herd, that they could not retrace their path to the corrals.

In both years, all observed cow-calf reunions took

place within the first 3 days. It may be that bonds not re-established within the first 2 - 4 days are lost. In other words, if anxiety over returning to the corrals area has kept the cow away for this period of time, she may not actively pursue the matter further.

Physiological Manifestations of Stress

Two days after the June 1976 roundup, one yearling was found in the pasture, crippled and unable to rise. Light coloured areas in the muscle of the hind limb seemed to indicate capture myopathy.

Although little is known of the etiology of the disease, the incidence of capture myopathy is characteristically highest whenever animals experience considerable psychological and/or physiological stress. Capture myopathy is commonly associated with over-exertion as when animals are chased over long distances and at high speeds. However, it has also been known to occur when over-exertion is not present. One possible explanation is that psychological stress (shock, fear, anxiety) is a sufficient factor but that over-exertion and exhaustion enhance susceptibility (Basson and Hofmeyr 1975).

Since capture myopathy usually occurs from within 1 to 14 days of handling stress, it was arranged that the 1977 subsample of bison could be kept for up to this period of time. One day after being processed, 8 animals were

observed to have a faltering gait. It was suspected to be the early signs of capture myopathy. However, after 1 week, no signs whatsoever remained. It was decided that detaining the animals further would not be justifiable.

One possible case of capture myopathy was documented in 1976. No cases were seen in 1977. Admittedly, a smaller number of animals was processed in 1977, and in any case, the difference between the occurence of capture myopathy in 1976 and 1977 is certainly not statistically significant. Yet the bison were observed for a much longer period in 1977. Can any significance be given to the fact that no capture myopathy was seen the second year? The question should be of interest to anyone involved in animal handling. Presence of the disease reflects physiological and/or emotional stress and thereby is indicative of poor management.

The helicopter roundup of the bison on the meadows appeared no less severe in 1977 than in 1976. Warden L. Callingwood (personal communication) believed that the animals in 1977 were pushed as hard if not harder than in 1976. Observations showed that animals were at times chased up to 5-6 km before being sorted and run out of the main pasture. It is possible that a certain amount of handling and running prior to the vaccination day may habituate the animals both physiologically and psychologically to later stress. To the best of my knowledge, however, this has not been documented in the literature.

The only physiological measurements recorded were rectal temperature and respiratory rate (Table 12).

TABLE 12. RESPIRATORY RATES AND RECTAL TEMPERATURES

AGE/SEX CLASS	RESPIRATORY RATE (Per minute)		RECTAL TEMPERATURES (Degrees C)
	1976	1977	1977 only
Bulls	100-125	48-80	39.3-41.8
Cows	118-132	30-72	39.2-42.0
Subadults	115-138	50-100	39.4-41.8
Calves	120-135	120-140	

However they could not, as planned, be used as indicators of changes in emotionality during the various phases of the vaccination procedure because rates remained at high levels throughout the operation. The calves especially, had greatly elevated respiratory rates. Similar rates were recorded at Elk Island National Park during a bison transplant project (personal observation). Calves there apporached 160 in their rate of breathing. Normal resting respiratory rates in bison are in the order of 60 per minute.

Two factors seemed likely to have led to the absence of capture myopathy in the second year. (1) In 1976, handling of the animals was accompanied by a great deal of noise and vigorous prodding (especially on the part of the many observers present). As a result of recommendations made that year, handling in 1977 was accomplished by fewer individuals and in a much more quiet manner. The animals moved more smoothly through the chutes and there was, for example, none of the fear-induced catatonia experienced in 1976.

Perhaps more important, (2) the ambient temperature during the first year rose to 20 degrees Celsius and there was no cloud cover. The second year however, the weather was overcast with occasional light showers and the ambient temperature averaged only 12.7 degrees C.

Hyperthermia has been noted as a pre-disposing factor in the incidence of capture myopathy (Basson and Hofmeyer 1975, Chalmers and Barret 1977). Rectal temperatures were therefore taken to determine whether the animals were hyperthermic during handling. In 1976 temperatures were not taken consistently, but those recorded were as high as 43.5 degrees C in the chutes. 1977 temperatures (Table 11), were without exception, lower. Hyperthermia may have been a problem during the first but not during the second year.

The facilities at Sweetgrass Meadows lend themselves to safe and efficient processing of bison. Yet emphasis solely

on facilities construction often leads to overly rough and thoughtless handling. Although there is a need to process the animals quickly, the techniques employed to acheive this may be stress inducing in themselves. The psychological impact of the situation should be remembered. Each bison is faced with a large number of humans well within its normal flight distance, and yet having nowhere to flee. In order to keep the animals calm and thereby facilitate an orderly flow, the aim of the handlers should be to present as low a profile as possible. Sharp, loud shouts will likely act to stop animals (Baskin 1974). An effort should be made to maintain a reduced noise level and try to stimulate only individual problem animals rather than shouting at the group as a whole. As discussed in the previous chapter, wild bison do not need the same handling methods as domestic cattle. They will respond to much more subtle stimuli if not completely confused or immobilized by panic.

CHAPTER SIX

SYNTHESIS

The purpose of this chapter is to review the findings of the study. Each chapter has been relatively discrete, and it is therefore important to understand how each section has helped to answer the questions being asked.

A considerable amount of interest is now being shown concerning the husbandry of native ungulates in some form of mixed-species grazing system. If these as yet non-domestic species are to be kept successfully, it is desirable that information be collected on the reactions of such ungulates to handling and management.

Basically, the questions I asked myself were:

1) What problems regarding management and handling does the keeping of wild ungulates pose? What barriers are there to their domestication?

2) Are there problems related to species-typical behaviour of various ungulate species which have prevented them from being husbanded in the past?

My working hypothesis was that few differences in species-specific behavioural responses exist as significant deterrents to the domestication or husbandry of wild ungulates.

I found the issue to be an extremely broad one. Three distinct approaches were taken to answer the questions that I asked. In Chapter 1, the approach taken was to investigate

the historic and pre-historic record. Have other species been considered for domestication in the past? For what reasons did any attempts fail? These questions were approached from the point of view of human paleo-economics. Changes in the nature of man-animal relaionships and in the types of ungulate species relied upon were explained as changes in ecological pressures upon human societies. The conclusions to this section were:

1) Ungulate species other than modern domestic ones were very likely husbanded by man in the pre-Neolithic period (e.g. red deer, moose, fallow deer, gazelle).

2) The shift to modern domestic species can be explained largely by reference to changes in patterns of resource exploitation by human societies during the early Neolithic.

3) As a result, it appears that those species husbanded and then abandoned by man may have been ecologically, but not necessarily behaviourally unsuited to further domestication.

In Chapter 2, a zoologically oriented analysis was performed. I collated available information on ungulate characteristics that might have influenced the likelihood of being selected for husbandry, or of doing well in captivity. Ungulates were divided into three groups, either domestic, wild or a third group including those species probably husbanded at some time in the past but not considered a domestic species today. Traits thought to be important to the analysis included Typical Group Size, Male

Mating System, Typical Social Unit, Feeding Style, Habitat Type, Body Weight, and Conformation. A statistical analysis, Multivariate Nominal Scale Analysis (Andrews and Messenger 1973), was carried out to determine which traits distinguished species that were conventionally domesticated from those which were not. The conclusions I drew were:

1) Certain important characteristics were identified as having historically favoured domestication. In brief, these traits were large body weight (over 50 kg), non-selective feeding styles, open country and montane habitats, non-territoriality, and typically large groups sizes.

2) Transient domestics did not follow any clear pattern. Selective and non-selective feeding,open and closed habitat, territorial and non-territorial, gregarious and solitary, each is represented among animals having been husbanded at some time in the past. This fact I interpreted to mean that inherent species-specific characteristics probably did not represent significant obstacles to husbandry. Our present agricultural system reflects certain ecological biases, and in turn, ungulate species seem to have been kept or discarded on the basis of food/habitat requirements.

In Chapter 3, a review was carried out over the literature on the ontogeny of behaviour in mammals. Topics dealt with included the effects of domestication on behaviour, the relative importance of hereditary and environmental influences, the importance of early experience to later behaviour, and problems posed by the captive

envrionment. Pertaining to the influence of domestication on behaviour, I tentatively accepted the argument that genetic alterations may be limited in their effect on mammal behaviour to (1) neoteny through a retention of neuron plasticity to a later age and (2) changes in nervous system thresholds such that responses are only elicited at higher stimulus levels.

To gain further and first hand information on behavioural responses of some related wild and domestic ungulate species, experimental work was carried out at the University of Alberta Experimental Farm using for the most part bison, yak and Hereford cattle. This work is reported in Chapter 4. Among the prime objectives were evaluation of habituation/sensitization to routine handling, determination of the effects of handling on performance factors (e.g. weight gain, feed intake), and observing relationships between species. Comparing a non-domestic species (bison) with a domestic species (Hereford cattle) it was found that:

1) Bison retained a much higher level of alertness to any visual or audible stimuli.

2) Maintenance of routine was more important to bison than to Herefords.

3) The degree of habituation and taming that was achieved in the case of the bison, was very specific to their daily handlers.

4) Peer group bonds appeared to be stronger among bison than

cattle.

On the basis of my results, I concluded that the differences between bison and Hereford cattle were largely quantitative rather than qualitative, and that these differences can be interpreted in terms of lower neural thresholds in non-domestic ungulates.

In summary, I maintain that few ungulate species have been ignored or abandoned by man because of inherent, species-specific characteristics irreconcilable with domestication. The implication is that contemporary experiments in domestication should not be approached with the pessimism that most wild ungulates are unsuited to husbandry. If an attempt is warranted economically and ecologically, then success depends largely on the flexibility and correctness of the management system employed. Those abnormalities of behaviour that do arise are more likely a result of unsatisfacotry captive conditions than any incompatibility with captivity itself.

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APPENDIX 1

Listing of MNA Data Deck

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	species)L
2	3	3	3	6	100	2	6	2	3	3	23	3	1	2	4	2	WART-HOG
1	3	2	1	6	90	2	5	5	2	5	23	3	3	2	1	1	SWINE
1	3	2	1	6	150	2	5	5	2	5	23	3	1	2	1	1	WILDBOAR
1	5	2	1	5	495	5	4	1	3	3	9	2	2	5	2	2	BISON
1	5	2	1	5	400	4	4	1	3	3	9	2	1	4	1	2	WISENT
1	5	2	1	5	500	4	4	1	3	3	9	2	3	5	1	2	CATTLE
1	4	2	1	6	103	3	4	1	3	6	10	2	1	3	2	3	BIGHORN
1	4	2	1	6	50	3	4	1	3	6	10	2	2	3	2	3	MOUFLON
1	4	2	1	6	110	3	4	1	3	6	10	2	1	1	1	3	URIAL
1	4	2	1	6	70	3	4	1	3	6	10	2	3	3	1	2	SOY SHEEP
1	4	2	1	6	60	3	4	2	3	6	10	2	2	3	1	3	IBEX
3	4	2	3	1	30	3	11	6	3	7	10	2	1	3	1	1	CHAMOIS
1	4	2	3	6	60	3	4	6	3	7	10	2	3	3	1	2	GOAT
1	3	1	3	6	74	2	1	6	3	7	10	2	1	1	2	1	MTN. GOAT
1	3	3	1	4	350	3	3	3	4	9	10	3	2	2	2	2	MUSK-OX
3	4	2	1	1	800	2	4	2	4	2	9	2	3	3	5	2	WATER BUFFALO
1	5	2	1	6	680	4	4	1	3	5	9	2	2	5	5	2	GAUR
1	5	2	1	5	290	3	4	1	3	6	9	2	3	4	1	2	YAK
1	5	2	1	5	300	3	4	1	3	5	9	2	2	4	5	2	BANTENG
1	1	2	1	5	600	2	1	4	4	4	14	3	1	2	4	1	GIRAFFE
1	1	1	6	0	250	2	1	4	2	5	13	3	1	1	4	1	OKAPI
2	3	3	2	5	1300	3	7	2	4		24	3	1	2	4	1	HIPPOPOTAMUS
2	5	3	3	5	22	2	6	2	1	5	26	3	1	2	3	1	PECCARY
3	3	2	2	1	180	3	1	6	3	5	1	3	1	3	5	1	NILGAI
1	3	2	1	4	35	3	3	1	3	3	15	1	1	4	1	2	SAIGA
2	2	1	3	2	7	1	8	5	2	5	18	1	2	1	5	1	CHINESE WATER DEER
2	1	1	3	6	25	1	8	5	2	5	16	1	1	1	5	1	MUNTJAC
2	3	1	3	6	10	1	8	6	6	7	22	1	1	1	1	1	MUSK DEER
1	3	2	3	2	30	2	10	6	2	2	19	1	1	2	3	1	PAMPAS DEER
2	1	1	3	6	100	2	8	7	2	4	17	1	1	2	5	2	CHITAL
2	1	1	3	6	225	1	8	7	2	5	17	1	1	1	5	2	SAMBAR
1	4	1	3	5	250	3	0	6	2	8	17	1	1	3	5	2	BARASINGHA
3	1	1	3	2	25	2	8	4	2	5	19	1	2	2	1	1	ROE DEER
1	4	2	2	6	45	0	0	4	2	5	17	1	2	3	1	3	FALLOW DEER
1	4	2	3	4	175	2	0	6	3	5	17	1	2	2	1	3	RED DEER
1	4	2	3	4	270	3	0	6	3	6	17	1	2	3	2	3	WAPITI
1	1	1	2	6	402	0	4	5	4	5	20	3	2	1	1	3	MOOSE
1	4	2	3	6	95	4	6	6	3	9	21	2	3	5	1	3	REINDEER
1	4	2	3	6	95	4	6	6	3	9	21	2	1	5	2	3	CARIBOU
1	1	1	3	6	92	2	0	4	2	5	19	1	1	2	1	2	MULE DEER
1	1	1	3	6	73	2	0	4	2	5	19	1	1	2	1	2	WHITE TAIL DEER
2	1	1	3	6	70	0	8	7	2	5	17	1	2	3	5	2	SIKA DEER

0	0	0	0	0	180	0	0	0	2	8	17	1	2	0	5	3	PERE DAVID DEER
2	5	3	2	3	45	1	9	3	3	6	25	2	1	3	3	1	VICUNA
1	4	2	2	4	68	3	4	3	3	6	25	2	1	3	3	1	GUANACO
1	4	2	2	4	85	3	4	3	3	6	25	2	3	4	3	1	LLAMA
1	4	2	2	4	65	3	4	3	3	6	25	2	3	4	3	1	ALPACA
1	3	2	3	4	600	3	0	3	4	1	25	2	3	4	1	1	DROMEDARY
1	3	2	3	4	500	3	0	3	4	1	25	2	3	3	1	1	BACTRIAN CAMEL
3	3	2	3	1	46	4	11	3	3	3	11	2	1	3	2	2	PRONGHORN
1	3	3	3	5	4200	3	2	7	4	4	30	3	3	3	5	2	INDIAN ELEPHANT
1	3	3	1	5	4500	5	2	6	4	5	30	3	2	5	4	3	AFRICAN ELEPHANT
2	1	1	2	1	4000	1	13	2	4	3	28	3	1	1	4	3	WHITE RHINO
2	1	1	2	1	3500	1	10	4	4	3	28	3	1	1	4	2	BLACK RHINO
2	1	1	2	6	2500	1	10	4	4	4	28	3	1	1	5	1	INDIAN RHINO
3	3	2	2	1	300	4	11	1	3	3	29	2	1	2	4	1	WILD-ASS
3	3	2	2	1	270	3	11	1	3	3	29	2	2	0	1	1	ONAGER
3	3	2	2	1	340	3	11	1	3	3	29	2	1	4	1	1	KIANG
1	3	3	2	4	270	3	3	1	3	6	29	2	1	3	4	1	MTN. ZEBRA
1	3	3	2	4	270	4	3	1	3	3	29	2	1	3	4	1	PLAINS ZEBRA
3	3	2	2	1	350	4	11	1	3	3	29	2	1	2	4	1	GREVY'S ZEBRA
1	3	3	2	4	350	4	3	1	3	3	29	2	3	3	1	1	HORSE
2	1	1	2	6	200	1	8	7	2	5	27	2	2	1	3	1	TAPIR
1	3	2	1	5	700	5	5	7	4	3	1	1	2	5	4	3	GIANT ELAND
1	3	2	1	5	650	5	5	7	4	3	1	1	2	5	4	3	CAPE ELAND
1	2	2	1	7	220	5	11	4	1	5	1	1	1	2	4	2	BONGO
1	3	2	1	7	250	3	11	4	2	4	1	1	1	2	4	3	GREATER KUDU
1	2	2	1	7	80	2	11	4	2	4	1	1	1	2	4	3	LESSER KUDU
1	3	2	1	7	220	3	11	4	3	6	1	1	1	3	4	2	MTN. NYALA
1	3	2	1	7	115	3	11	4	2	4	1	1	1	3	4	2	NYALA
1	1	1	1	7	125	2	11	5	1	8	1	1	1	2	4	2	SITATANGA
2	1	1	3	1	55	2	8	5	1	5	1	1	1	1	4	1	BUSHBUCK
3	3	2	2	1	103	4	10	3	3	1	2	1	2	5	4	3	ADDAX
3	3	2	2	1	204	4	10	3	3	1	2	1	2	5	4	3	SCIMITAR ORYX
3	3	2	2	1	168	5	10	3	3	3	2	1	2	5	4	3	BEISA ORYX
3	5	2	2	1	204	5	10	3	3	3	2	1	2	5	4	3	GEMSBOK
3	3	2	2	1	250	4	10	2	3	3	2	1	1	3	4	3	ROAN
3	3	2	2	1	216	3	11	2	2	4	2	1	1	3	4	3	SABLE
3	3	2	1	1	216	3	11	2	3	3	3	1	1	3	4	3	DEFASSA
3	3	2	1	1	204	3	11	2	3	3	3	1	1	3	4	3	WATERBUCK
4	3	2	1	1	80	3	12	2	3	2	3	1	1	5	4	2	KOB
3	3	2	1	1	91	3	11	2	3	2	3	1	1	3	4	2	PUKU
3	4	2	1	1	116	3	11	2	3	0	3	1	1	3	4	2	LECHWE
3	3	2	1	1	86	3	11	2	3	2	3	1	1	3	4	2	NILE LECHWE
2	2	1	1	2	43	2	9	2	3	2	3	1	1	2	4	1	BOHOR-REEDBUCK
2	3	1	1	1	66	2	10	2	3	2	3	1	1	2	4	1	SOUTHERN-REEDBK
2	2	2	1	1	25	2	9	1	3	6	3	1	1	2	4	1	MTN-REEDBUCK
2	3	2	1	2	23	2	10	2	3	6	3	1	1	2	4	1	RHEBUCK
3	3	2	3	3	166	4	11	1	3	3	4	1	1	5	4	2	BUBAL
3	3	2	3	1	170	4	11	1	3	2	4	1	1	5	4	2	RED HARTBEEST
3	3	2	3	1	132	4	11	1	3	3	4	1	1	5	4	2	LICHT HARTBEEST
3	3	2	3	1	116	4	11	1	3	3	4	2	1	3	4	2	TOPI
3	3	2	3	1	149	4	11	1	3	2	4	2	1	5	4	2	TSESSEBE
3	3	2	3	1	80	4	11	1	3	2	4	2	1	3	4	2	BLESBOK
3	3	2	3	1	73	4	11	1	3	3	4	2	1	5	4	2	HUNT HARTBEEST

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3 4 2 3 1  216 4 11 2 3 3  4 2 1 5 4 2 BRINDLED GNU
3 4 2 3 1  160 4 11 2 3 2  4 2 1 5 4 2 BLCK WILDEBEEST
2 3 1 3 1   45 2 10 4 2 4  5 1 1 2 4 1 GERENUK
3 2 1 3 1   31 2 11 4 2 4  5 1 1 2 4 1 DIBATAG
3 3 2 3 3   65 3 11 6 2 3 12 1 1 3 4 2 IMPALA
3 3 2 3 1   73 3 11 7 2 1  5 1 1 3 4 1 DAMA GAZELLE
3 4 2 2 1   45 3 11 7 2 3  5 1 1 3 4 1 SOEM GAZELLE
3 3 2 2 3   62 3 11 7 3 2  5 1 1 5 4 2 GRANTS GAZELLE
3 3 2 0 1   22 3 11 7 3 1  5 1 1 3 4 2 DORCAS GAZELLE
3 3 2 0 1   18 3 11 7 3 1  5 1 1 3 4 2 PELZELN GAZELLE
3 3 2 3 1   27 3 11 7 3 1  5 1 1 3 4 2 LODERS GAZELLE
3 3 2 3 1   28 3 11 7 3 1  5 1 1 3 4 2 RED FRONTED GAZLE
3 3 2 3 1   18 3 11 7 2 2  5 1 1 3 4 2 SPEKES GAZELLE
3 3 1 3 1   25 3 11 6 2 2  5 1 1 3 4 2 THOMPSONS GAZELLE
3 3 2 2 1   34 3 11 7 2 2  5 1 1 3 4 2 SPRINGBUCK
2 1 1 3 1   55 1  8 5 1 5  6 1 1 1 4 1 YELLOW BACK DUIKER
2 1 1 3 1   64 1  8 5 1 5  6 1 1 1 4 1 JENTINKS DUIKER
2 1 1 3 1   57 1  8 5 1 5  6 1 1 1 4 1 ABBOTTS DUIKER
2 1 1 3 1   12 1  8 5 1 5  6 1 1 1 4 1 BLACK DUIKER
2 1 1 3 1   13 1  8 5 1 5  6 1 1 1 4 1 BANDED DUIKER
2 1 1 3 1   13 1  8 5 1 5  6 1 1 1 4 1 ZEBRA DUIKER
2 1 1 3 1   18 1  8 5 1 5  6 1 1 1 4 1 PETERS DUIKER
2 1 1 3 1   14 1  8 5 1 4  6 1 1 1 4 1 RED DUIKER
2 1 1 3 1   20 1  8 5 1 5  6 1 1 1 4 1 BAY DUIKER
2 1 1 3 1   18 1  8 5 1 5  6 1 1 1 4 1 GABON DUIKER
2 1 1 3 1   20 1  8 5 1 5  6 1 1 1 4 1 OGILBYS DUIKER
2 1 1 3 1   18 1  8 5 1 5  6 1 1 1 4 1 BLACK FRONT DUIKER
2 1 1 3 1    7 1  8 5 1 5  6 1 1 1 4 1 BLUE DUIKER
2 1 1 3 1   12 1  8 5 2 3  6 1 1 1 4 1 GRIMMS DUIKER
2 1 1 3 1    4 1  8 5 2 5  7 1 1 1 4 1 ROYAL ANTELOPE
2 1 1 3 1    5 1  8 5 2 5  7 1 1 1 4 1 PYGMY ANTELOPE
2 1 1 3 2    8 1  9 5 2 4  7 1 1 1 4 1 SUNI
2 2 1 3 2   15 2  9 2 3 2  7 1 1 2 4 1 ORIBI
2 2 1 3 2   16 1  9 5 3 7  7 1 1 1 4 1 KLIPSPRINGER
2 1 1 3 1   14 1  8 7 3 2  7 1 1 1 4 1 STEENBOK
2 1 1 3 2    9 1 10 4 1 4  7 1 1 1 4 1 SHARPES GRYSBOK
2 1 1 3 2   11 1 10 6 1 4  7 1 1 1 4 1 CAPE GRYSBOK
2 3 1 3 2   27 1  9 5 2 6  8 1 1 1 4 1 BEIRA
2 2 1 3 2    4 1  9 5 2 4  8 1 1 1 4 1 GUENTHERS DIKDIK
2 2 1 3 2    5 1  9 5 2 4  8 1 1 1 4 1 KIRKS DIKDIK
2 2 1 3 2    4 1  9 5 2 4  8 1 1 1 4 1 PHILLIPS DIKDIK
1 4 2 1 5  320 5  4 2 4 4  9 3 1 5 4 2 FOREST BUFFALO
1 4 2 1 5  820 5  4 2 4 3  9 3 1 5 4 2 CAPE BUFFALO
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BEHAVIOURAL CHARACTERISTICS OF HOOFED MAMMALS

Key to Variable Categories

A) SPATIAL ARRANGEMENT

1. non exclusive use of space
2. exclusive all purpose territories
3. mating only territories
4. lek

B) SOCIAL UNIT COMPOSITION (index of sociability)

1. single
2. pair
3. single males, nursery bands, and bachelor groups
4. aggregations with seasonal segregation of males
5. aggregations with little seasonal segregation

C) FEMALE ALLIANCE

1. loose
2. intermediate
3. stable

D) SCENT MARKING (socially significant, principal type)

1. none
2. urine/dung
3. specialized gland

E) MALE MATING SYSTEM

1. territorial individual males
2. territorial pair
3. territorial harem
4. non-territorial harem
5. rank
6. roving
7. intermediate forms of territorial males

F) BODY WEIGHT (kg)

1. 0-10
2. 11-30
3. 31-50
4. 51-200
5. 201-500

6. 501-10,000

G) JARMAN'S SOCIAL CLASSES (Jarman 1974, with some modifications)

-includes territorial and non-territorial forms-

1. live singly or in pairs (Jarman's class A)
2. typical group size one to twelve (class B)
3. typical group size six to sixty (class C)
4. typical group size six to a few hundred - may aggregate into super-herds (class D)
5. permanent large herds (class E)

H) LEUTHOLD'S SOCIAL CLASSES (Leuthold 1977)

1. -individuals, no lasting associations
2. Non-exclusive
   -stable nursery bands, loose bachelor groups
3. home range
   -stable harmes, bachelor groups
4. -large, stable mixed herds, and bachelor groups
5. -no lasting associations, nursery bands, solitary males
6. Non-exclusive
   -small, stable nursery bands with
   home range
   temporarily associated males
7. but exclusive
   -large nursery bands, males separate
   home site.

8. Exclusive home
   -individuals only
   range
9. in both sexes.
   -permanent pairs
10. All purpose
    -small nursery bands, solitary adult
    male territory
    males, bachelor groups
11. male mating
    -variable nursery groupings, solitary adult territory males, bachelor groups
12. Lek territory
    -variable nursery groupings, solitary adult males, bachelor groups
13. All purpose male
    -females in small bands or solitary,

territory with
solitary territorial and dominant,
hierarchy
males, subordinate satellite males

I) FEEDING STYLES (after Leuthold 1977)

1. roughage grazers
2. fresh grass grazers dependent upon water
3. dry region grazers with some dicotyledons
4. tree and shrub foliage browsers
5. fruit and dicotyledonous foliage selectors
6. intermediate feeders preferring grasses
7. intermediate feeders preferring forbs and tree foliage

J) ANTIPREDATOR BEHAVIOUR

1. avoid detection
2. flight after detection and before attack
3. flight under attack
4. threatening or even attacking predator

K) HABITAT TYPE

1. desert
2. grassland/flood plain
3. savanna
4. bush
5. forest
6. montane
7. alpine
8. swamp
9. tundra

L) TAXONOMIC GROUP

1. Tragelaphinae
2. Hippotraginae
3. Reduncinae
4. Alcelaphinae
5. Antilopinae
6. Cephalophinae
7. Neotraginae
8. Madaquinae
9. Bovinae
10. Caprinae
11. Antilocaprinae
12. Aepyceratinae
13. Okapiinae
14. Giraffinae
15. Saiginae
16. Muntiacinae

17. Cervinae
18. Hydropotinae
19. Odocoileinae
20. Alcinae
21. Rangiferinae
22. Moschinae
23. Suidae
24. Hippopotamidae
25. Camelidae
26. Tayassuidae
27. Tapiridae
28. Rhinocerotidae
29. Equidae
30. Proboscidae

M) POST-NATAL MOTHER-YOUNG RELATION

1. hider
2. follower
3. defender

N) STATUS WITH RESPECT TO DOMESTICATION

1. no evidence of any husbandry
2. historically transient or current experimental husbandry
3. classical domestic species

O) TYPICAL GROUP SIZE

1. 1-3
2. 1-15
3. 1-50
4. 1-100
5. 100+

P) FAUNAL REGION

1. Palearctic
2. Nearctic
3. Neotropical
4. Ethiopian
5. Oriental

Q) CEPHALIZATION OF DISPLAY

1. negligible
2. moderate
3. extreme

LITERATURE SURVEYED:

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